The Journal of ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY

VOLUME 31 2003 NUMBER 2

The Journal of Arachnology (ISSN 0161-8202), a publication devoted to the study of Arachnida, is published three times each year by *The American Arachnological Society.* **Memberships (yearly)**: Membership is open to all those interested in Arachnida. Subscriptions to *The Journal of Arachnology* and *American Arachnology* (the newsletter), and annual meeting notices, are included with membership in the Society. Regular, $40; Students, $25; Institutional, $125 . Inquiries should be directed to the Membership Secretary (see below). **Back Issues**: Patricia Miller, P.O. Box 5354, Northwest Mississippi Community College, Senatobia, Mississippi 38668 USA. Telephone: (601) 562-3382. **Undelivered Issues:** Allen Press, Inc., 1041 New Hampshire Street, P.O. Box 368, Lawrence, Kansas 66044 USA.

Cover photo: Theotima minutissimus with spiderlings. Photo by Robert L. Edwards, Wood's Hole, Massachusetts.

Publication date: 03 October 2003

♾ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

2003. The Journal of Arachnology 31:157–172

SPIDERS OF THE GENUS *TETRAGNATHA* (ARANEAE, TETRAGNATHIDAE) IN THE SOCIETY ISLANDS

R.G. Gillespie: Division of Insect Biology, University of California Berkeley, 201 Wellman Hall, Berkeley, CA 94720-3112, USA.

ABSTRACT. This study revises the status of knowledge of the spider fauna of the Society Islands. Until recently, the literature on the spider fauna in these islands has suggested that the genus *Tetragnatha* in particular is noticeable for its poor representation in comparison with the large radiation in the Hawaiian Islands. Expeditions were conducted to determine whether this genus is indeed poorly represented in the islands as the literature would suggest. The results indicate that the islands actually have a number of endemic *Tetragnatha*, although there is no noticeable adaptive radiation as is seen in the Hawaiian Islands. Results of field expeditions in 1999–2000 and studies on historical collections have shown that: (1) Reports of the cosmotropical species *T. mandibulata* in the Society Islands are probably not valid; these were misidentifications for either *T. macilenta* or *T. nitens*. (2) *Tetragnatha huahinensis* is a synonym of *T. macilenta*. (3) There are three new species of *Tetragnatha*, all of which are described here and appear to be endemic to middle and high elevations of the Society Islands (from Tahiti, Moorea and Raiatea). In total, there are six species of *Tetragnatha* in the Society Islands: in addition to the three endemic species there is one possibly indigenous (*T. macilenta*), and two that may be of more recent introduction (*T. nitens* and *T. maxillosa*).

Keywords: Tahiti, Moorea, Pacific, descriptions, biogeography

The Society archipelago consists of six high islands (Fig. 1). The archipelago is remote, 400 km from the nearest island group and 6,000 km from the nearest continental landmass (Australia). In common with the other remote Polynesian archipelagoes of Hawaii and the Marquesas, the Society Islands are all volcanic in origin and formed as volcanic hot spots. All three archipelagoes exhibit a chronological arrangement of islands. In Hawaii, the islands range from Kauai, the oldest in the north at 5.1 myrs, to Hawaii, the youngest in the south at up to 0.4 myrs old. The Society Islands range from Bora Bora, the oldest in the north at 3.3 myrs, to Tahiti, the youngest in the south at 1.0 myrs. The similarity between the islands of Hawaii, the Marquesas and Societies is not limited to their geological history, but may also extend to certain elements of the indigenous arthropod fauna (Meyrick 1935).

To date, knowledge of the spider fauna of the Society Islands has shown little in common with the Hawaiian Island chain, though it has been very little studied. What is known can be attributed largely to the initial efforts of L. Koch (1872) and subsequent work by Berland (1927, 1929, 1933, 1934a, 1934b, 1934c, 1935a, 1935b, 1935c, 1938, 1942) from the Muséum National d'Histoire Naturelle (MNHN) in Paris, with some of this information being summarized by Marples (1957). Berland (1934b) described knowledge of the spider fauna of Tahiti as follows (in translation):

"In spite of its universal prestige, especially in literary work, the fauna of this archipelago is poorly known. In all, there are approximately 15 known species as follows: *Pholcus ancoralis*, *Cyrtophora viridipes*, *Araneus theisi*, *Heteropoda regia*, *Corinna cetrata*, *Thorellia ensifera*, *Plexippus paykulli*, *Bavia aericeps*, *Athamus whitmeei*, *Mollica microphthalma and pusilla*, *Hasarius albocircumdatus*, *Ascyultus pterygodes*, and *Lauharilla insulana*. It is obviously very little: there is almost no trace of endemism. Given what is known of archipelagoes close to the Societies, and that the species above are clearly Polynesian (excluding cosmopolitans, of course), one can conclude that Tahiti has not been sufficiently explored. It is not possible currently to affirm a real poverty of fauna, and we should await other investigations. What is significant above all, it is that the islands fit well in the Polynesian group."

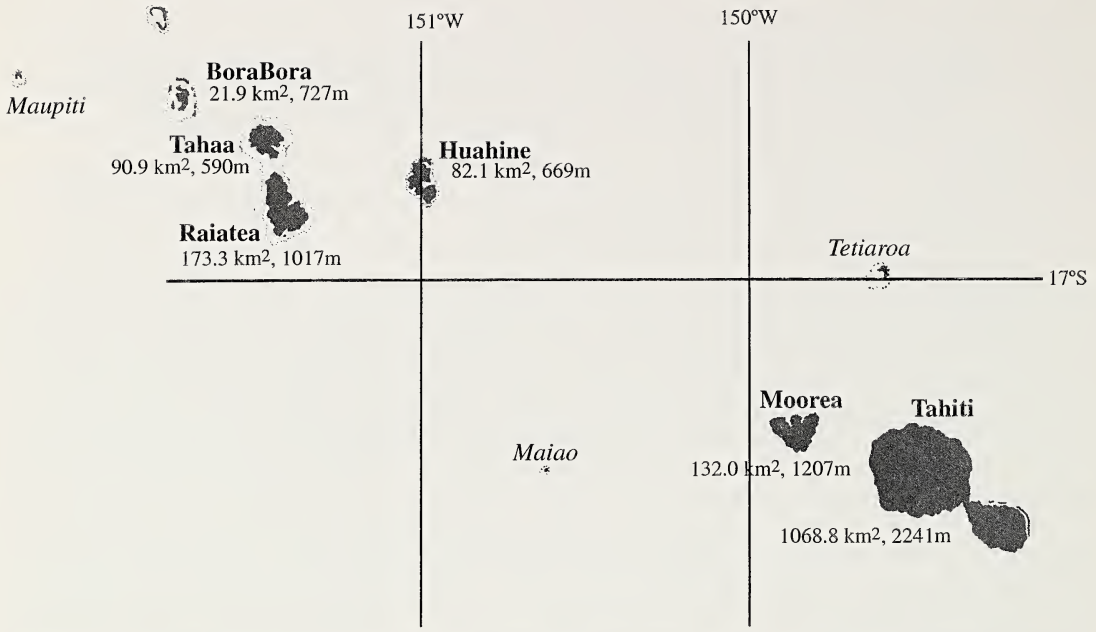


Figure 1.—Map of the Society Islands. Area and elevation are given for each of the main islands.

This statement is a reasonable reflection of the knowledge of the spider fauna of the Society Islands (Marples 1957) before the expeditions in which I was involved in 1999–2000. Prior to these expeditions, the only species of *Tetragnatha* reported from the Society Islands were *T. macilenta* L. Koch, *T. huahinensis* Berland, *T. maxillosa* Thorell, and *T. mandibulata* Walckenaer. The only reported endemic was *T. huahinensis*. The current study set out to reassess the distribution of *Tetragnatha* in the islands and determine whether the lack of representation was due to insufficient collecting, or whether it represented a real paucity of species.

I have now collected on Tahiti, Moorea, Raiatea, and Bora Bora. I have also examined collections at the MNHN, the Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB), the British Natural History Museum, London (BMNH), and the Bishop Museum, Honolulu (BPBM).

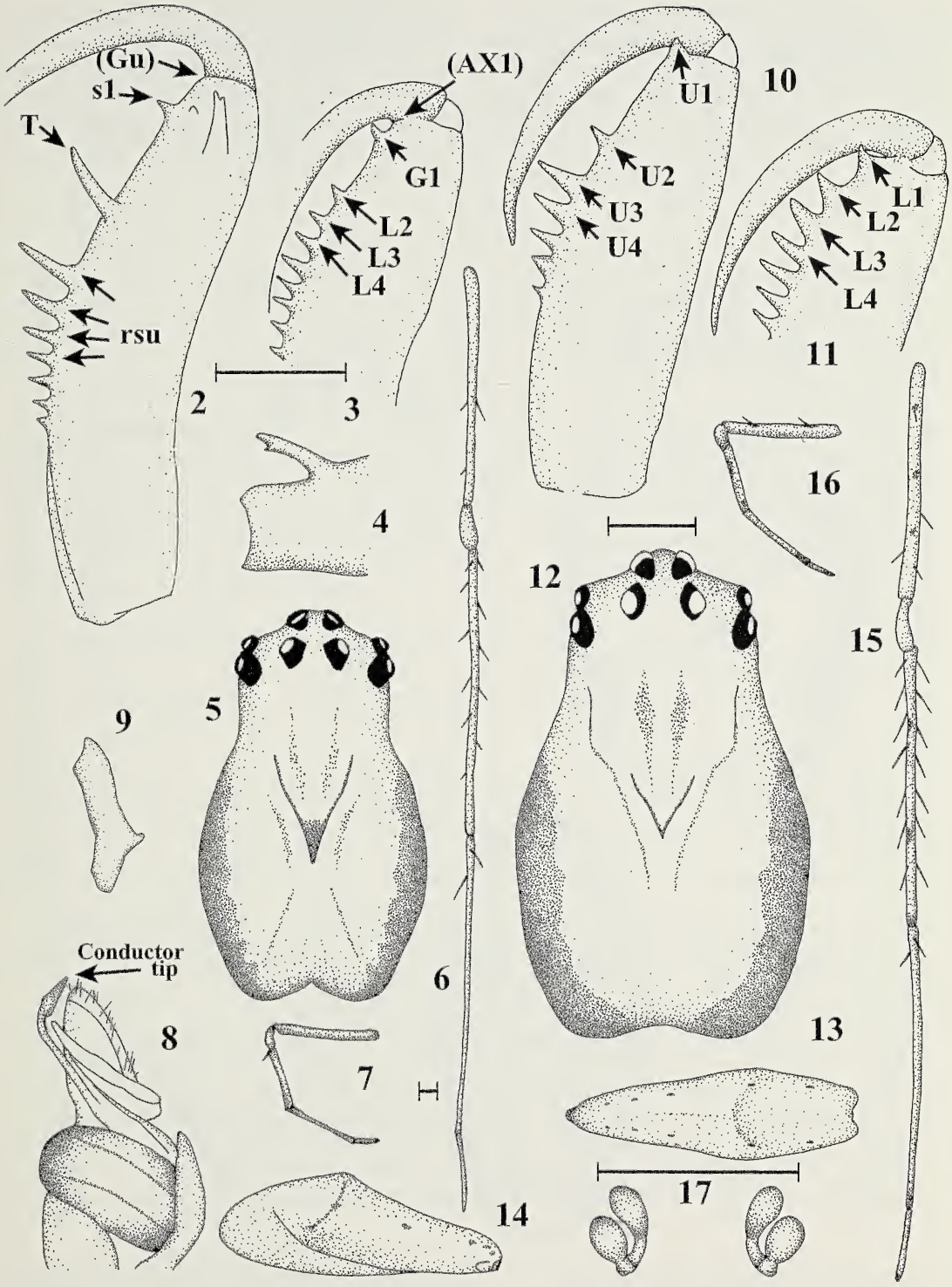
METHODS

Characters examined.—Morphological measurements taken were the same as those described in Gillespie (1991): genital morphology, arrangement of eyes; cheliceral tooth pattern; form and setation of the first and third legs; and form and pattern of the dorsum and carapace. In order to estimate variability within a taxon and determine which features best characterize a species, where possible measurements were taken on six individuals of each sex of each species with additional observations on other individuals once diagnostic characters had been identified.

Terminology.—The terminology for the teeth on the cheliceral margins of the males is that used in previous papers (Gillespie 1991; Figs. 2, 3, 8, 10, 11). Setation on femora, tibiae and metatarsi of legs I & II is denoted by: fI, fIII, tI, tIII, mI and mIII. CITR refers to the cheliceral inter-tooth ratio, the ratio of 3 lengths: (1) between distal end of male chelicerae to sl; (2) sl to T; and (3) T to rsul. All new holotypes have been deposited in the BPBM and all paratypes will be deposited in the Essig Museum of Entomology of the University of California, Berkeley (EMUC). Most of the recent collections were performed by the author (RGG) and George Roderick (GKR). Unless indicated otherwise, all measurements are in mm.

DISCUSSION

Three new species of *Tetragnatha* that appear to be endemic to the Society Islands are described: *T. rava, T. moua*, and *T. tuamoaa*.



Figures 2–17.—*Tetragnatha rava*: Male holotype. 2. Promargin of right chelicera; 3. Retromargin of left chelicera; 4. Dorsal spur of right chelicera, lateral; 5. Carapace, dorsal; 6. Right leg I, dorsal; 7. Right leg III, prolateral; 8. Left palpus, ventral; 9. Left paracymbium, lateral. Female allotype. 10. Promargin of right chelicera; 11. Retromargin of left chelicera; 12. Carapace, dorsal; 13. Abdomen, dorsal; 14. Abdomen, lateral; 15. Right leg I, dorsal; 16. Right leg III, prolateral; 17. Seminal receptacles, ventral. Scale bars = 0.5; that between Figs. 2 & 3 applies to Figs. 2, 3, 4, 10 & 11; above Fig. 12 applies to Figs. 5 & 12; between Figs. 6 & 7 applies to Figs. 6, 7, 13, 14, 15 & 16; at Fig. 17 applies to Figs. 8, 9 & 17.

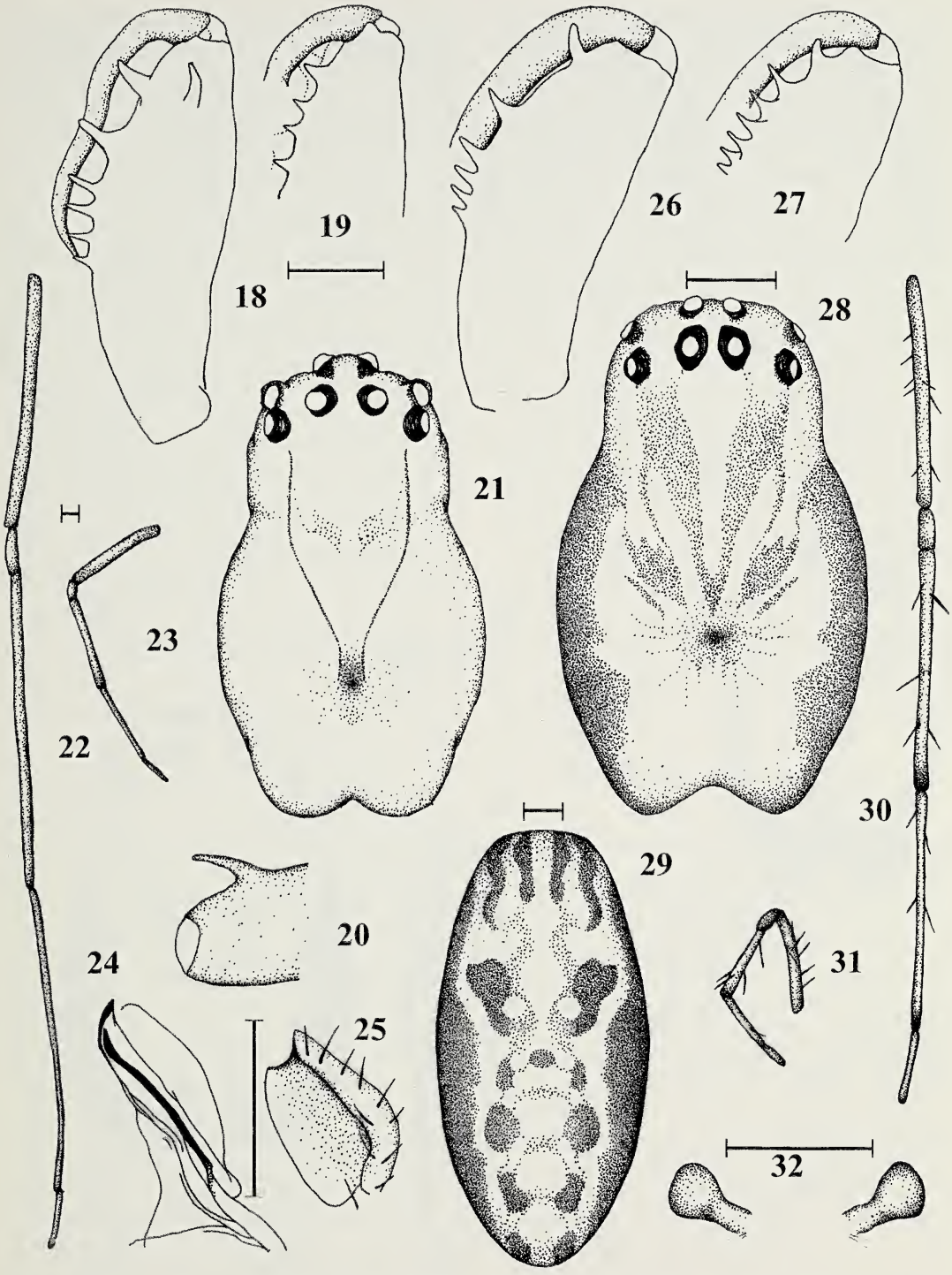
There are three additional species in the archipelago, none of which is endemic; *T. macilenta* is widely distributed in the western Pacific; it may be indigenous to the Society Islands. *T. maxillosa* and *T. nitens* are also widely distributed from the tropical Pacific, and these may represent more recent introductions. Other designations of species to the Society Islands appear to be incorrect. There is no indication that *T. laqueata* or *T. mandibulata* occur in the islands. *T. huahinensis*, which was described as a new species unique to the island of Huahine, appears to be a synonym of *T. macilenta*.

KEY TO SPECIES

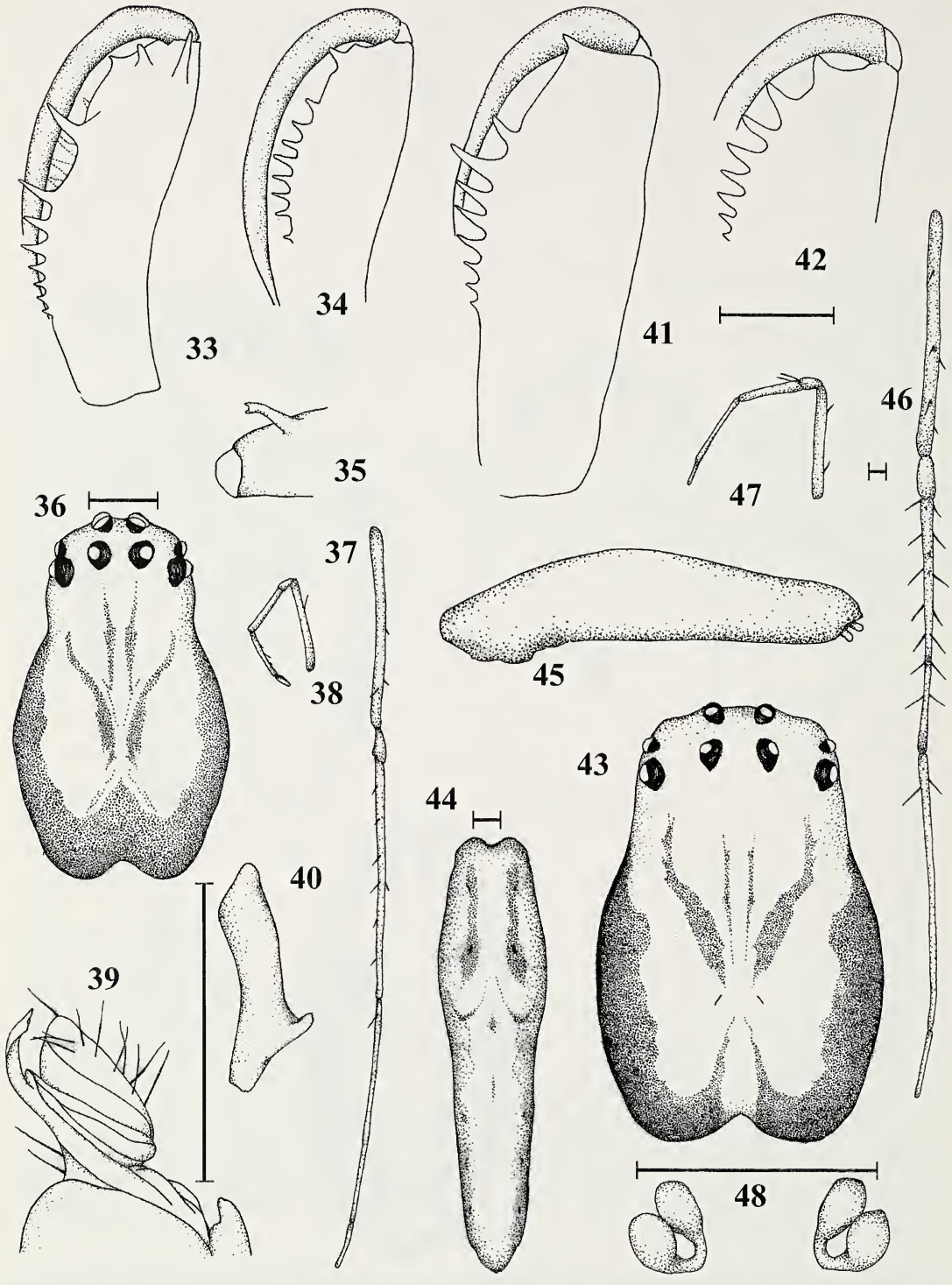
1. Anterior and posterior eye rows strongly recurved (Figs. 65, 72); abdomen very long, 6–10 times as long as broad (Figs. 66, 77) ..... *T. macilenta*
   Anterior and posterior eye rows not strongly recurved (Figs. 5, 12, 21, 28, 36, 43); abdomen ≤ 4 times as long as broad 2
2. Males 3
   Females 7
3. Dorsal spur of chelicerae and first two marginal teeth (s1 and T) all large and clustered near apex of chelicerae (Levi 1981, p. 299, fig. 31; Okuma 1987, p. 84, fig. 31a) .. *T. nitens*
   Dorsal spur of chelicerae and first two marginal teeth not clustered (Figs. 2, 18, 33) 4
4. First two marginal teeth (s1 and T) large, much longer than remaining marginal teeth, and well separated; conductor cap broad and hooked, shaped much like the head of a vulture (Okuma 1987, p. 83, fig. 30 a & b). ..... *T. maxillosa*
   s1 similar in length (Fig. 18) or smaller (Figs. 2, 33) than at least first of remaining marginal teeth (rsu) 5
5. First large marginal tooth (s1) similar in size to second (T) (Fig. 18). Conductor broad, with a very slight curl at tip (Fig. 80) ..... *T. moua*
   First marginal tooth (s1) much smaller than second (T) (Figs. 2, 33). Conductor curved over well below tip (Figs. 79, 81) 6
6. Conductor pointed at tip (Fig. 79) ..... *T. rava*
   Conductor rounded at tip (Fig. 81) ..... *T. tuamoaa*
7. Very strong apical teeth on both upper and lower margins of chelicerae, projecting out (approximately at right angles) from cheliceral margin (Okuma 1987, p. 83, figs. 30e, f) ..... *T. maxillosa*
   Apical teeth similar in size or smaller than remaining cheliceral teeth (Figs. 10, 26, 41) 8
8. Prominent tooth at apex of underside of chelicerae pointing straight up, parallel to cheliceral margin (Levi 1981, p. 299, fig. 25; Okuma 1987, p. 84, fig. 31 h) ..... *T. nitens*
   No prominent tooth at apex of underside of chelicerae (Figs. 10, 26, 41) 9
9. Abdomen little more than 2× as long as broad (Fig. 29). ALEs similar in size to PLEs (Fig. 28). Seminal receptacles single large bulbs (Fig. 32) ..... *T. moua*
   Abdomen approximately 4× as long as broad (Figs. 13, 44). ALEs smaller than PLEs (Figs. 12, 43). Seminal receptacles with two lobes (Figs. 17, 48) 10
10. Anterior median eyes closer together than posterior median eyes (Fig. 12); connection between bulbs of seminal receptacles long, looped below lower bulb (Fig. 17) ..... *T. rava*
    Anterior median eyes about same distance apart as posterior median eyes (Fig. 43); connection between bulbs of seminal receptacles fairly short, direct (Fig. 48) ..... *T. tuamoaa*

Tetragnatha rava new species
(Figs. 2–17, 79)

Type data.—Holotype male from Tahiti: Tahiti Iti, Mt. Teatara, 650m, 17.79°S, 149.25°W, 7 July 2000, RGG and GKR (BPBM). Paratypes (all in EMUC): Tahiti: 2 males, 2 females, 1 immature, Belvedere: 580 m, 17.57° S, 149.56°W, 19 November 1999, RGG; 2 males, 2 females, 12 immatures, Tahiti Iti, Mt Teatara, 650 m, 17.79° S, 149.25°W, 7 July 2000, RGG and GKR.



Figures 18–32.—*Tetragnatha moua*: Male holotype. 18. Promargin of right chelicera; 19. Retromargin of left chelicera; 20. Dorsal spur of right chelicera, lateral; 21. Carapace, dorsal; 22. Right leg I, dorsal; 23. Right leg III, prolateral; 24. Distal end of left palpus, ventral; 25. Left paracymbium, lateral. Female allotype. 26. Promargin of right chelicera; 27. Retromargin of left chelicera; 28. Carapace, dorsal; 29. Abdomen, dorsal; 30. Right leg I, dorsal; 31. Right leg III, prolateral; 32. Seminal receptacles, ventral. Scale bars = 0.5; that between Figs. 18 & 19 applies to Figs. 18, 19, 26 & 27; above Fig. 28 applies to Figs. 21 & 28; between Figs. 22 & 23 applies to Figs. 22, 23, 30 & 31; above Fig. 29 applies to Fig. 29; between Figs. 24 & 25 applies to Figs. 24 & 25.



Figures 33–48.—*Tetragnatha tuamoaa*: Male holotype. 33. Promargin of right chelicera; 34. Retromargin of left chelicera; 35. Dorsal spur of right chelicera, lateral; 36. Carapace, dorsal; 37. Right leg I, dorsal; 38. Right leg III, prolateral; 39. Distal end of left palpus, ventral; 40. Left paracymbium, lateral. Female allotype. 41. Promargin of right chelicera; 42. Retromargin of left chelicera; 43. Carapace, dorsal; 44. Abdomen, dorsal; 45. Abdomen, lateral; 46. Right leg I, dorsal; 47. Right leg III, prolateral; 48. Seminal receptacles, ventral. Scale bars = 0.5; that between Figs. 41 & 42 applies to Figs. 33, 34, 35, 41 & 42; above Fig. 36 applies to Figs. 36 & 43; between Figs. 46 & 47 applies to Figs. 37, 38, 46 & 47; that between Figs. 39 & 40 applies to Figs. 39 & 40; that above 44 applies to Figs. 44 & 45.

Etymology.—The specific epithet, regarded as a noun in apposition, is the Tahitian word for "brownish" and refers to the light brown coloration of these spiders.

Diagnosis.—*Tetragnatha rava* is most similar to *T. tuamoaa* on Moorea. It differs in having the two anterior median eyes closer together than the two posterior median eyes (Figs. 5 & 12), while the median eye pairs are similarly well separated in *T. tuamoaa*; by having a sharper point to the conductor of the male palp (Fig. 79 compared to Fig. 81); and by having a longer connection between the bulbs of the female seminal receptacles (Fig. 17, compare to Fig. 48).

Description.—*Holotype male:* (Figs. 2–9, 79) Length of carapace 2.2, total length 8.2. Chelicerae 94% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 2): Gu absent, but very small tooth present dorsal/lateral to sl; distance between apex and s1 much less than between s1 and T, CITR approx. 0.2:0.5:0.3; s1 small point, longer than wide (approximately half width and 25% height of T); T large, pointing slightly up and out from margin of chelicerae; rsu 7 straight spikes, decreasing in size. Retromargin of chelicerae (Fig. 3): total of 9 teeth; AX1 absent; G1 quite small and pointing straight up out, L2–L7 showing slight increase in size proximally until fourth to last tooth. Dorsal spur not long, straight (12% length of carapace); tip projecting dorsally (Fig. 4). Thoracic fovea distinctly marked around depression (Fig. 5). Coloration and eye pattern as in female. Leg setation similar to female (Figs. 6–7). Conductor (Figs. 8, 79): tip pointed and slightly curled back. Male paracymbium narrow with lateral projection, pointed at apex (Fig. 9).

Allotype female: (Figs. 10–17) Length of carapace 3.0, total length 11.0. Chelicerae 58% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 10): 7 teeth, U1 short, pointing straight up, slightly wider, shorter than U2 and well separated (25% cheliceral length) from U2; U2 short, U3 taller than other teeth; U4–U7 decreasing in size proximally. Retromargin of chelicerae (Fig. 11): series of 7 teeth: L1 slightly larger than U1, smaller than L2. Remaining retromarginal teeth decreasing slightly in length and width proximally. Posterior eyes half width of distance between them. Median ocular area wider posteriorly (Fig. 12); lateral eyes contiguous. Carapace brown with very pronounced markings including dark margins. Abdomen elongate, dilated at midline; dorsum light brown with paired markings down sides (Figs. 13, 14). Legs sparsely marked with occasional spots (Figs. 15, 16). Leg spines medium length and robust; setation: fI 1/3/2; tI 7/0/7; mI 1/1/0; fIII with 2 dorsal only, and tIII and mIII without macrosetae. Seminal receptacles (Fig. 17): narrow anterior bulb, slightly wider posterior bulb, connected by long loop.

Variation.—(n = 4♂, 4♀). Male: Cephalothorax 2.2–2.4. CITR little variation; rsu sometimes 6. Female: Length of carapace 3.0–3.3. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha rava* is found mostly at middle elevations (580 m at Belvedere–650 m on Tahiti Iti) on Tahiti. Because of the relatively low elevation at which it is found, its habitat tends to be disturbed, with mixed native and non-native vegetation. The animal has a "furry" appearance because of the macrosetae on its legs.

Tetragnatha moua new species
(Figs. 18–32, 80)

Types.—Holotype male from Tahiti: Mt. Aorai, 1700 m, 17.61° S, 149.50°W, RGG and GKR, 17 November 1999 (BPBM). Paratypes (all in EMUC): Tahiti: 2 males, 6 females, 6 immatures, Mt. Aorai 1700 m, 17.61° S, 149.50°W, 17 November 1999, RGG and GKR; 8 females, 2 immatures, Mt. Marau 1280 m, 17.61°S, 149.55°W, 6 July 2000, RGG and GKR; 2 males, 1 female, Mt. Marau 1240 m, 17.61°S, 149.54°W, 6 July 2000, M. Arnedo.

Etymology.—The specific epithet, regarded as a noun in apposition, is the Tahitian word for "mountain" and refers to the montane environment to which this species is restricted.

Diagnosis.—*Tetragnatha moua* is very distinct from all other species based on genital morphology (Figs. 24, 32, 80) and cheliceral armature (Figs. 18–20, 26, 27).

Description.—*Holotype male:* (Figs. 18–25, 80) Length of carapace 2.6, total length 6.4. Chelicerae 81% length of carapace. Cheliceral fang considerably shorter than base,

bent over at both proximal and distal ends and in middle. Promargin of chelicerae (Fig. 18): Gu absent; distance between apex and s1 slightly less than between s1 and T, CITR approx. 0.3:0.4:0.3; s1 large, longer than wide (approximately 1 $^2/_3$ and 90% height of T); T pointing straight out from margin of chelicerae; rsu 4 straight spikes, decreasing in size proximally. Retromargin of chelicerae (Fig. 19): total of 5 teeth; AX1 absent; G1 prominent but small and pointing straight up out, L2–L5 decreasing in size proximally. Dorsal spur fairly long, slightly bent (16% length of carapace); tip pointed (Fig. 20). Thoracic fovea distinctly marked around depression (Fig. 21). Coloration and eye pattern as in female. Legs almost completely devoid of setation (Figs. 22, 23). Conductor (Figs. 24, 80): tip broad, curled over at top, embolus surrounded by conductor, shorter. Paracymbium rounded with pointed apex (Fig. 25).

Allotype female: (Figs. 26–32) Length of carapace 2.8, total length 8.5. Chelicerae 70% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 26): 6 teeth, U1 long, curved up and out, similar in size to U2 and well separated (24% cheliceral length) from U2; U3–U6 decreasing in size proximally. Retromargin of chelicerae (Fig. 27): series of 7 teeth: L1 smaller than U1, similar in size to L2. Remaining retromarginal teeth decreasing very slightly in length and width proximally. Posterior eyes wider than distance between them. Median ocular area approximately square (Fig. 28); lateral eyes contiguous. Carapace brown with very pronounced markings including dark margins, and pair of dark lines running from behind PLE's and converging broadly towards fovea. Abdomen plump, elongate oval; dorsum dark brown with quite elaborate reddish markings down center and sides (Fig. 29). Legs sparsely marked (Figs. 30, 31). Leg spines medium length and quite robust; setation: fI 2/1/5; tI 2/1/3; mI 1/1/2; fIII with 4 dorsal, 2 prolateral, tIII with 2 dorsal, 2 prolateral, and mIII with no dorsal and 1 prolateral, macrosetae. Seminal receptacles (Fig. 32): pair of single large bulbs.

Variation.—(n = 4♂, 6♀).—Male: Cephalothorax 2.6–2.9. CITR little variation. Female: Length of carapace 2.7–2.9. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha moua* is a large, robust and colorful species with smooth legs (not furry) that occurs at upper elevations (above 600m) on both Mt. Aorai and Mt. Marau. Individuals frequently do not build webs, and are found at night, especially on Mt Aorai, foraging actively in the open. They are less common on Mt. Marau.

Tetragnatha tuamoaa new species
(Figs. 33–48, 81)

Types.—Holotype male, allotype female from Moorea: Trois Cocotiers, 320 m, 17.55°S, 149.50°W, M. Arnedo, 5 July 2000 (BPBM). Paratypes (all in EMUC): Moorea: 1 immature, Paopao-Vaiare 320 m, 17.52°S, 149.80°W, 19 June 2000, RGG; 1 female, 2 immatures, Paopao-Vaiare 320 m, 17.52°S, 149.80°W, 3 July 2000, M. Arnedo; 2 immatures, Trois Cocotiers, 320 m, 17.55°S, 149.50°W, 18 June 2000, RGG; 2 males, 1 female, 1 immature, Trois Cocotiers, 320 m, 17.55°S, 149.50°W, 5 July 2000, M. Arnedo.

Etymology.—The specific epithet, regarded as a noun in apposition, is the Tahitian word for "mountain ridge" and refers to the situations to which the species is confined on Moorea.

Diagnosis.—*Tetragnatha tuamoaa* is most similar to *T. rava* on Tahiti. It is distinguished by the separation of the AMEs, with the median ocular area almost square (Figs. 36 & 43); by the angular (not pointed) tip of the conductor (Fig. 81); and by the tighter connection between the bulbs of the seminal receptacles.

Description.—*Holotype male:* (Figs. 33–40, 81) Length of carapace 2.6, total length 9.0. Chelicerae 65% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 33): Gu absent, but prominent tooth (larger than sl) present dorsal/lateral to sl; distance between apex and s1 much less than between s1 and T, CITR approx. 0.2:0.4:0.4; s1 small, pointed slightly down, as wide as high (approximately 1/3 width and 22% height of T); T large, pointing slightly up and out from margin of chelicerae; rsu 7 straight spikes, decreasing in size. Retromargin of chelicerae (Fig. 34): total of 9 teeth; AX1 absent; G1 quite small and pointing straight up and out, L2- L7 showing slight increase in size proximally until fourth to last

tooth. Dorsal spur quite long, slightly bent (16% length of carapace); tip bifurcated (Fig. 35). Thoracic fovea distinctly marked around depression (Fig. 36). Coloration and eye pattern as in female. Leg setae shorter than female, but setation pattern similar to female (Figs. 37, 38). Conductor (Fig. 39, 81): tip broad, blunt, curled back. Paracymbium narrow, apex pointed (Fig. 40).

Allotype female: (Figs. 41–48) Length of carapace 3.0, total length 11.0. Chelicerae 65% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 41): 9 teeth, U1 short, pointing out, slightly wider, shorter than U2 and well separated (25% cheliceral length) from U2; U2 medium length, U3 taller than other teeth; U4–U7 decreasing in size proximally. Retromargin of chelicerae (Fig. 42): series of 8 teeth: L1 slightly broader than U1, smaller than L2. Remaining retromarginal teeth decreasing slightly in length and width proximally. Eyes small, posterior eyes half width of distance between them. Median ocular area almost square (Fig. 43); lateral eyes contiguous. Carapace brown with very pronounced markings including dark margins. Abdomen elongate, dilated at midline; dorsum light brown with paired markings down sides (Figs. 44, 45). Legs sparsely marked with occasional spots (Figs. 46, 47). Leg spines medium length and robust; setation: fI 0/3/2; tI 7/0/7; mI 1/0/1; fIII with 2 dorsal only, and tIII with 1 dorsal and mIII without macrosetae. Seminal receptacles (Fig. 48): fairly narrow anterior bulb, slightly wider posterior bulb, connected by robust loop.

Variation.—(n = 2♂, 4♀). Male: Cephalothorax 2.4–2.6. CITR little variation; rsu sometimes 6. Female: Length of carapace 2.9–3.2. Color patterns vary slightly; no polymorphism.

Natural history.—As in the low elevation *Tetragnatha rara* on Tahiti, *T. tuamoaa* has a "hairy" appearance. It is similar in gross morphology to *T. rava*, but its eye configuration, and male and female genitalia are distinct.

Other material examined (non-types).—Raiatea: 1♀, Opoa, approximately 16.83°S, 151.38°W, 1955, N. Krauss (BPBM).

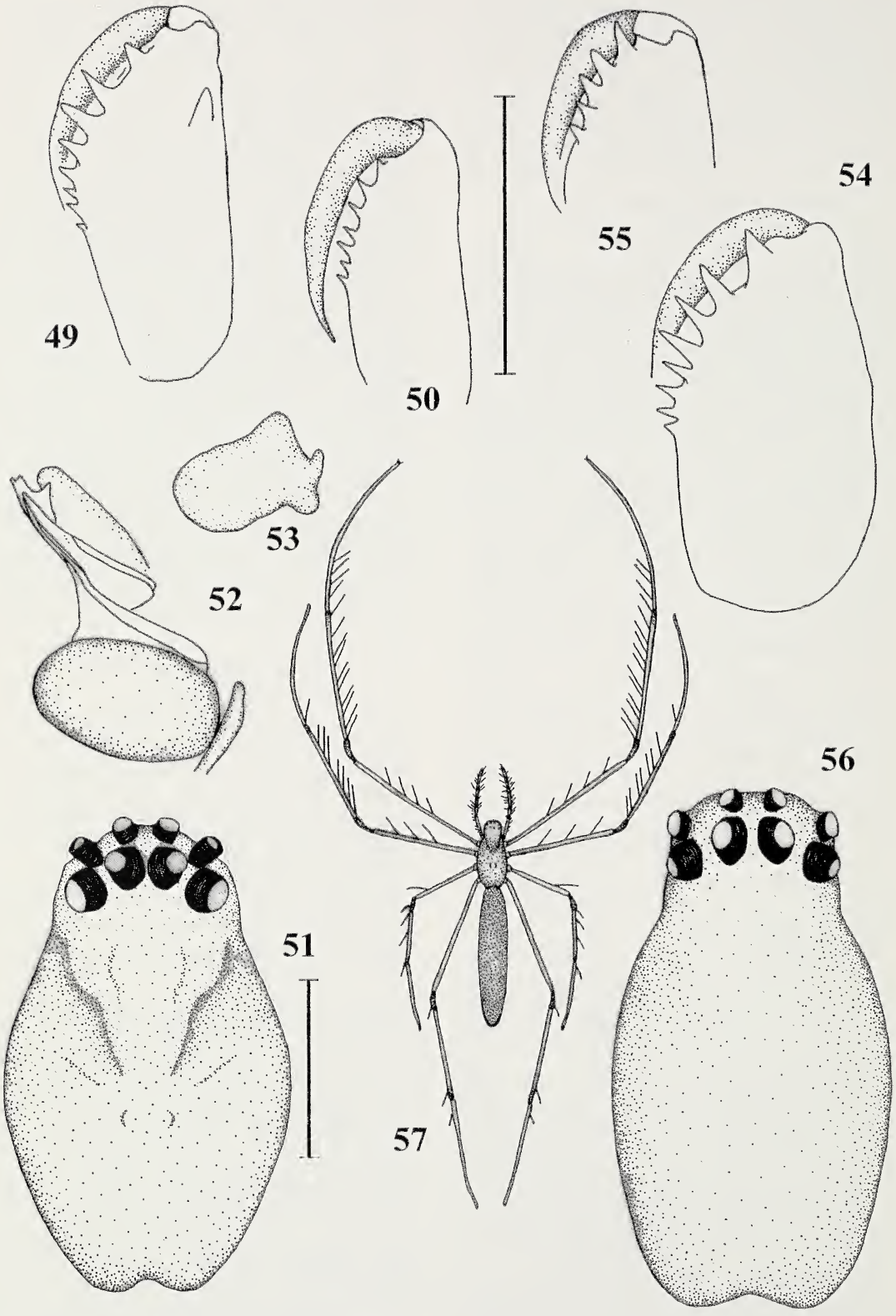
Remarks.—The female from Raiatea was identified as *T. laqueata* by Marples (1957), although Marples did state that "Identifications [were] more or less uncertain". This female is certainly not *T. laqueata*. *Tetragnatha laqueata* was first described by L. Koch from Upolu, Samoa. The type specimen was deposited in the Museum Godeffroy, which was mostly absorbed into the Museum für Naturkunde der Humboldt-Universität Berlin in Germany. I have examined 1 male and 3 female syntypes of *T. laqueata* collected from Upolu, Samoa, housed in the Museum für Naturkunde (Figs. 49–57). These specimens are *T. laqueata* as described by Koch (1872). However, since that time, *T. laqueata* has also been recorded from the Bonin Islands and elsewhere in the north Pacific. These latter records are likely to be incorrect: the specimens described by Okuma (1980) and Yaginuma (1979) are quite different from *T. laqueata* as described by Koch (1872). The single female specimen from Raiatea reported by Marples (1957) (BPBM) is most similar to *T. tuamoaa*. There are differences in the female genitalia. However, until a male specimen is found, I have adopted the more conservative approach to placing it in the same species as *T. tuamoaa*.

Tetragnatha macilenta L. Koch
(Figs. 58–78)

Tetragnatha macilenta L. Koch 1872: 192, T. XVI, fig. 6, T. XVII, fig. 1 (male syntype lost, two female syntypes from Upolu, Samoa, in ZMB, examined); Berland 1929: 60, figs. 45–51 (1 male, 2 females from Upolu, Samoa, in MNHN, examined); Roewer 1942: 986; Bonnet 1959: 4338; Okuma 1987: 63, fig. 16.

Tetragnatha huahinensis Berland 1942: 19, fig. 8 a–d (female holotype from Mt. Turi, Huahine, 16.72°S, 151.10°W, 1 October 1934, E.C. Zimmerman, in BPBM, examined). NEW SYNONYMY.

Types.—*Tetragnatha macilenta* was first described by L. Koch from Upolu, Samoa. The type was a male specimen and was supposed (L. Koch 1872) to have been deposited in the Museum Godeffroy, which, as mentioned above, was mostly absorbed into the ZMB. However, two females only remain at the ZMB. These females do appear to be *T. macilenta*, and are from Upolu, Samoa. However, there is also a male and female in the ZMB collection that were thought to be the syntypes of *T. macilenta* from New South Wales, Australia. These latter specimens are *T. valida* (not *T. macilenta*). In the BMNH, *T.*


49
50
55
54
53
52
56
51
57

macilenta L. Koch is represented by one male from the Solomon Islands (collected by Rennell); one male from the Cook Islands, Aitutaki; one male and one female in forest, Upolu, Samoa; and many specimens from Apia, Upolu, Samoa (most collected by Marples). However, although I have not studied the BMNH collection in any detail, the male type is not in this collection. Accordingly the location of the type, if it still exists, is currently unknown.

Synonymy.—Berland (1942) described a new species, *T. huahinensis*, from Huahine. However, this specimen appears to be *T. macilenta* (Figs. 63–66). Berland describes *T. huahinensis* as follows (in translation): "Female (no male) color light brown, margin and two stripes darker, labium brown, sternum light, margin gray; abdomen gray with little silver plates on sides and, in posterior half, 2 rows of 4 small brown spots. Both eye rows recurved, first a little more, eyes nearly equal in size, anterior lateral a little smaller, lateral of two rows a little farther from each other than median. Chelicerae with strong tooth near fang. Abdomen long, about 10× as long as wide. Total length 12mm. Society Islands, Huahine, Mt. Turi, alt. 600–700ft, Oct. 1 1934, one female holotype". Berland goes on to say "I think that *T. huahinensis* is well characterized by the length of the abdomen and by the peculiar form of the chelicerae." Interestingly, Berland (1929) drew a very similar diagram when discussing *T. macilenta* L. Koch from Upolu, Samoa. What is more, comparison of the type of *T. huahinensis* (as illustrated in Berland 1942) with the illustrations shown here of *T. macilenta* (Figs. 58–78) leaves little doubt that *T. huahinensis* is a synonym of *T. macilenta*.

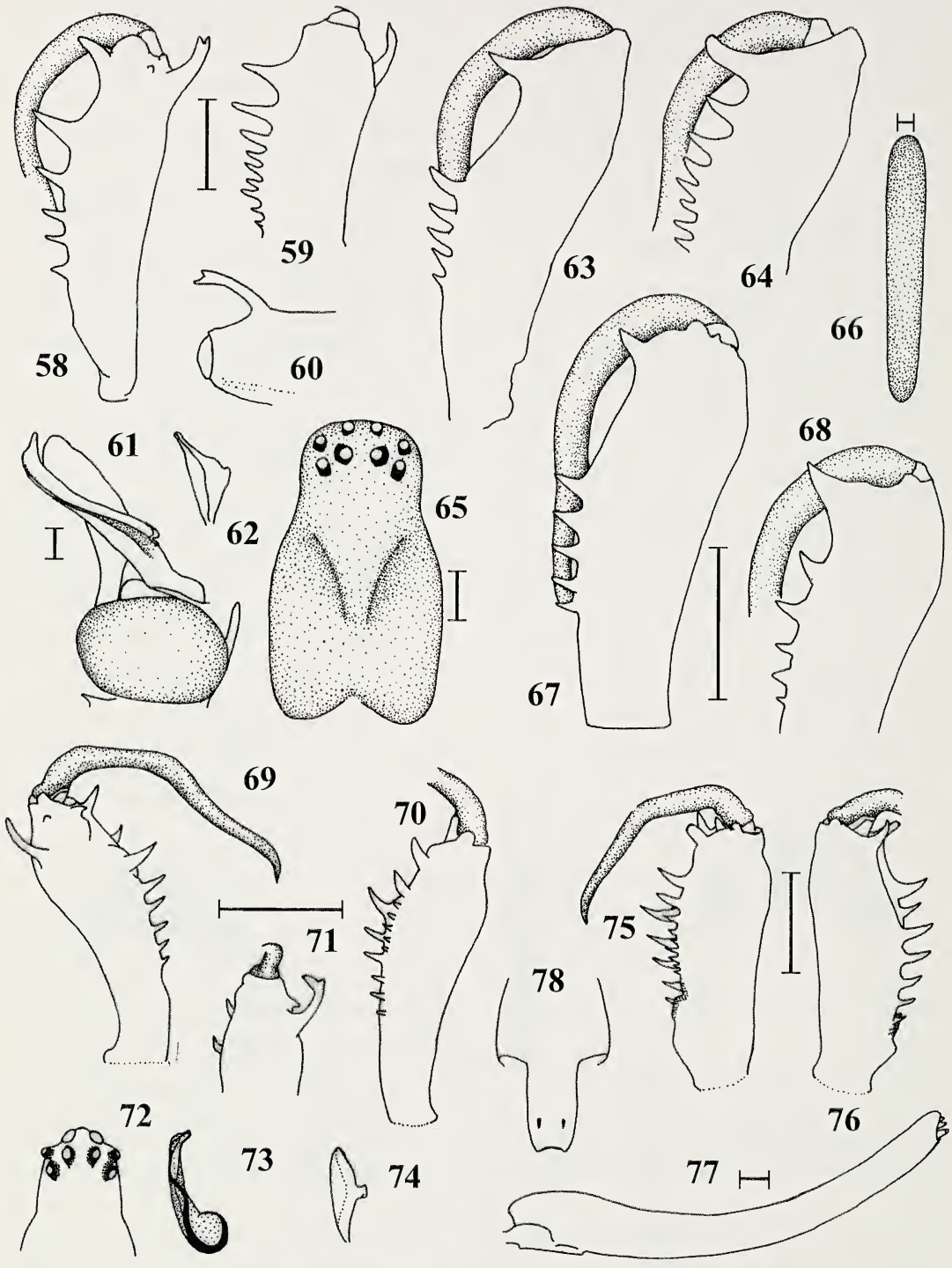
Material examined.—In the Society Islands, *T. macilenta* has been collected from Tahiti: 1♂,1 immature, Vaipaarii, 600 m, August 1928, Samson (labeled *T. mandibulata* by Berland); 2♂, 4♀, 8 immatures, Mt. Marau 790–1240 m, 17.60°S, 149.57°W, July 2000, RGG and GKR; 1♂, 3 immatures, Mt Aorai 1700 m, 17.61° S, 149.50°W, November 1999, RGG and GKR; Moorea: 2♂, 6♀, 2 immatures, Trois Cocotiers, 320 m, 17.55°S, 149.50°W, June 2000, RGG and GKR; 4♀, 4 immatures, Mouaputa, 450 m, 17.53°S, 149.80°W, July 2000, GKR; Raiatea: 1♀, Temehani, 700 m, 16.78°S, 151.45°W, September 1977, WC Gagne; Bora Bora: 2♀, 16.45° S, 151.87° W, July 2000, M. Arnedo.

Remarks.—*Tetragnatha macilenta* appears to be widespread through Polynesia, although not as widespread as the literature would suggest. Roewer (1942) cited L. Koch (1872) and Berland (1929) in describing the distribution of the species as Norfolk Island, Samoa, Marianas, Tonga, Marquesas Islands, and Hawaii. However, neither Koch nor Berland mention Hawaii, so the inclusion of Hawaii is likely a publication error. Moreover, the records from the Marquesas are based on the publications of Berland (1933, 1935b). Examination of museum specimens (BPBM, MNHN) has shown that all the specimens from the Marquesas that were labeled as *T. macilenta* are in fact other species.

Subsequently, Bonnet (1959) cited the distribution of *T. macilenta* as Samoa, Norfolk Island, and Marquesas, reflecting accurately the work of L. Koch (1872), Karsch (1878) and Rainbow (1920) who documented the species from Samoa and Norfolk Island. Subsequently, Chrysanthus (1975) examined specimens from New Guinea and the Bismarck Archipelago, but cited Roewer (1942) and Bonnet (1959) in stating that it is "further known from Norfolk Island, Hawaii and Marquesas Islands." Most recently, Okuma (1987) stated that *T. macilenta* is found from Australia, New Guinea, Solomon Is., Norfolk Is., Samoa, Marianas, Tonga, Marquesas and Hawaii. However, the specimens she examined were all from Australia, New Guinea, Solomons, Tonga, New Britain, and Admiralty Is-

←

Figures 49–57.—*Tetragnatha laqueata*: Male and female syntypes collected from Upolu, Samoa, currently in the Museum für Naturkunde der Humboldt-Universität Berlin. Male: 49. Promargin of right chelicera; 50. Retromargin of left chelicera; 51. Carapace, dorsal; 52. Left palpus, ventral; 53. Left paracymbium, lateral. Female. 54. Promargin of right chelicera; 55. Retromargin of left chelicera; 56. Carapace, dorsal; 57. *T. laqueata* redrawn from Koch (1872). Scale bars = 0.5; that between Figs. 50 & 55 applies to Figs. 49, 50 & 52–55; that beside Fig. 51 applies to Figs. 51 & 56.



Figures 58–78.—*Tetragnatha macilenta*: 58–62. Male from Temehani Pl (700m), Raiatea, Society Islands, collected by W. Gagne (4 September 1977). 58. Promargin of right chelicera; 59. Retromargin of left chelicera; 60. Dorsal spur of right chelicera, lateral; 61. Left palpus, ventral; 62. Left paracymbium, lateral. 63–66. Female from Huahine, Society Islands, 500–700m, collected by E. Zimmerman (1 October 1934; drawn from type female of *T. huahinensis* Berland). 63. Promargin of right chelicera; 64. Retromargin of left chelicera; 65. Carapace, dorsal; 66. Abdomen, dorsal. 67, 68. *T. macilenta* syntype female

lands. She did not examine any Polynesian species, instead referring to L. Koch (1872), Berland (1929), Roewer (1942) and Chrysanthus (1975). I therefore conclude that *T. macilenta* has not been found further east than the Society Islands.

Figures 58–78 compare specimens of *T. macilenta*, with Figs. 58–62 a specimen from Raiatea, Figs. 63–66 the female type of *T. huahinensis* from Huahine, and Figs. 67, 68 the female syntype of *T. macilenta* from Upolu, Samoa (ZMB). Note the similarity between Figs. 63 and 67, and 64 and 68. Figs. 69–78 show the general features of *T. macilenta* from Australia, New Guinea, Solomon Islands, Tonga, Admiralty Islands, New Britain, and Samoa, redrawn from Okuma (1987).

Tetragnatha maxillosa Thorell

Tetragnatha mandibulata Walckenaer: Thorell 1890: 221 (misidentification).
Tetragnatha maxillosa Thorell 1895: 139; Gravely 1921: 430; Roewer 1942: 984; Bonnet 1959: 4339; Chrysanthus 1975: 8, Figs. 14–21; Okuma 1983: 72; Okuma 1987: 83, fig. 30.
Tetragnatha maxillosa insignita Strand 1911: 138.

Material examined.—In the Society Islands, *T. maxillosa* has been collected from the following localities: Tahiti: 1♂,1 ♀*, Near Tiupi Bay, Papaari, 17.74° S, 149.34°W, sweeping grasses and low herbage, May 1934 (BPBM); 1♂, 2 ♀*, Papeete, 17.53° S, 149.37°W (BPBM); 1 ♀*, Tiarei, 17.55° S, 149.35°W; 1♂, 1 ♀*, Vallée de la Reine, 140 m, 17.54° S, 149.40°W, December 1928 (BPBM); 3♂, 2♀, Papenoo Valley 195 m, 17.55° S, 149.43°W, July 2000, RGG and GKR; Moorea: 3♀, 2♂, Trois Cocotiers, 220 m, 17.55°S, 149.50°W, over stream, June 2000, RGG and GKR (EMUC); Raiatea: 1 ♀*, Uturoa, 16.80°S, 151.45°W; 1 ♀, Temehani Plateau, 427 m, 16.78°S, 151.45°W, October 1934, E.C. Zimmerman (BPBM); 2 ♂, 3 ♀, same data except 800m, over stream, July 2000, RGG and GKR (EMUC); 1 immature, Opoa (BPBM). (* det. C. Okuma, confirmed by author; all others determined by author).

Remarks.—*Tetragnatha maxillosa* was first described by Thorell (1895) from Java, and reported also from Burma, Malaya and India. Chrysanthus (1975) redescribed and illustrated the species and recorded it from New Guinea for the first time. There is a good deal of confusion because Thorell (1895) first described the species based on a specimen that he had initially (Thorell 1890) misidentified as *T. mandibulata* Walckenaer (see below). Berland used the name "*T. mandibulata* Koch, not Walckenaer" for specimens that in almost all cases appear, upon recent examination by C. Okuma and myself, to be *T. maxillosa* (see below).

Tetragnatha nitens (Audouin)

Eugnatha nitens Audouin in Savigny 1826: 118, Pl. 2, fig. 2 (specimens from Rosetta, Egypt, lost).
Eugnatha pelusia Audouin in Savigny, 1826: 119, pl. 2, fig. 3 (specimen from Rosetta, Egypt, lost).
Tetragnatha andina Taczanowski 1878: 144, pl. 1, fig. 2.
Tetragnatha antillana Simon 1897: 868; Seeley 1928: 104, figs. 1–4; Roewer 1942: 988; Chickering 1957: 306, figs. 1–6; Bonnet 1959: 4318; Chickering 1962: 428, figs. 1–6.
Tetragnatha vicina Simon 1897: 869.
Tetragnatha peninsulana Banks 1898: 246, pl. 15, fig. 12.
Tetragnatha galapagoensis Banks 1902: 61, pl. 1, fig. 10.
Tetragnatha aptans Chamberlin 1920: 41, figs. 7, 8.
Tetragnatha eremita Chamberlin 1924: 645, figs. 89, 90.
Tetragnatha seminola Gertsch 1936: 10, figs. 22, 23.
Tetragnatha steckleri Gertsch & Ivie 1936: 19, figs. 31–33.
Tetragnatha elmora Chamberlin & Ivie 1942: 62, fig. 160.

←

from ZMB. 67. Promargin of right chelicera; 68. Retromargin of left chelicera. 69–78. *T. macilenta* redrawn from Okuma (1987). 69–74 Male. 69. Promargin of left chelicera; 70. Dorsal spur of left chelicera; 71. Retromargin of left chelicera; 72. Eye group of male; 73. Conductor and embolus; 74. Left paracymbium, lateral. 75–78 Female. 75. Promargin of left chelicera; 76. Retromargin of left chelicera; 77. Genital fold of female. 78. Abdomen, lateral. Scale bars = 0.5; that between Figs. 58 & 59 applies to Figs. 58, 59, 60, 62, 63 & 64; that between Figs 67 & 68 applies to Figs. 67 & 68. Figs. 69–78—scale bars inferred from text where possible; that between Figs. 69 & 70 applies to Figs. 69, 70 & 71; that between Figs. 75 & 76 applies to Figs. 75 & 76.

Tetragnatha festina Bryant 1945: 407, figs. 38, 39, 41.

Tetragnatha haitensis Bryant 1945: 408, fig. 37.

Tetragnatha nitens (Audouin): Bonnet 1959: 4345; Levi 1981: 291, plate 5a–b, figs. 23–34; Okuma 1968: 40, figs. 9–16; Okuma 1983: 75; Okuma 1987: 84, fig. 31; Roewer 1942: 978.

Material examined.—In the Society Islands, *T. nitens* has been collected only from Moorea: 1 female, Baie de Cook, 0 m, 17.50°S, 149.82°W, March 1955, Krauss (BPBM); 8 males, 10 females, Gump Field Station in mangroves, 0 m, 17.49°S, 149.83°W, November 1999, RGG and GKR (EMUC).

Remarks.—*Tetragnatha nitens* is found along the coast of Moorea. This species has a huge distribution and is said to be "cosmotropical" (Platnick 1997). It may not be native to the Society Islands.

Tetragnatha mandibulata Walckenaer

Tetragnatha mandibulata Walckenaer 1837: 211.

Tetragnatha mandibulata (Walckenaer): Roewer 1942: 984; Bonnet 1959: 4338; Chrysanthus 1963: 733, figs. 24–26, 36–39; Chrysanthus 1975: 6; Okuma 1983: 70; Okuma 1987: 85, fig. 32.

Remarks.—As mentioned above, there has been much confusion regarding this species, perhaps based on the inadequacy of the initial description. The species was described by Walckenaer (1837) as follows (in translation): "Mandibles carried in front, very-prominent, very-elongate, dilated at the middle, divergent, and whose base terminates in a spine or hook* of a red blade. Cylindrical abdomen, elongate, narrower than the cephalothorax, a little bent or raised in the posterior part, color drab green. The cephalothorax is elongate, reddish, bordered by a fine yellow line. The palpi and the legs are red. There are grayish or white hairs on the cephalothorax, the legs, and the mandibles. From the Marianas archipelago, Guam, collected by M. Freycinet." (* the spine is believed to refer to the first stout tooth of the ventral row, which extends directly forward beside the base of the fang,

←

Figs. 79–81.—High magnification photographs of distal tips of conductor of male palps. 79. *T. rava*; 80. *T. moua*; 81. *T. tuamoaa*.

Chrysanthus 1975). L. Koch (1872) drew what he thought to be *T. mandibulata*. However, it was clear that he was uncertain, as he labeled the specimen "*Tetragnatha mandibulata* Walck.? ". Subsequently, the specimens that Berland examined have been ascribed to L. Koch rather than Walckenaer, but appear to be *T. maxillosa* (see above). The confusion with *T. mandibulata* has been summarized by Chrysanthus (1975), who notes:

"*Tetragnatha mandibulata* sensu Keyserling, 1865 = *T. keyserlingi* Simon (Simon 1890) p. 134.

Tetragnatha mandibulata sensu L. Koch 1871 = *T. kochi* Thorell (Thorell 1895) p. 140

Tetragnatha mandibulata sensu Thorell 1890 = *T. maxillosa* Thorell (Thorell 1895) p. 139."

Note that Thorell (1895) assigned the specimens that L. Koch examined to *Tetragnatha kochi*. As Chrysanthus (1975) notes "the differences between these three species are small, and their identification requires careful examination; it may be, therefore, that some records in the arachnological literature are incorrect." Certainly, all specimens that I have examined (and Okuma before me) that have been assigned to "*T. mandibulata* Koch, not Walckenaer" are *T. maxillosa*. I conclude, therefore, that there are no confirmed records of *T. mandibulata* in French Polynesia. However, *T. mandibulata* is found in Hawaii, Micronesia, the Philippines, and Australia through to West Africa (Platnick 1997).

ACKNOWLEDGMENTS

I am greatly indebted to the Délégation de la Recherche in Tahiti for allowing access to collecting sites. In particular, I am most grateful to Jean-Yves Meyer for helping with the immense problems of logistics. I also express my sincere thanks to Christine Rollard (Muséum National d'Histoire Naturelle, Paris), Jason Dunlop (the Museum für Naturkunde der Humboldt-Universität, Berlin), Paul Hillyard (the Natural History Museum, London), and Gordon Nishida and David Preston (the Bishop Museum, Honolulu). Finally, I am hugely indebted to Lesley Pankaew, a very talented young art student at the University of California at Berkeley, for her help with the drawings. The manuscript was much improved by comments from Herb Levi and Mark Harvey.

LITERATURE CITED

Audouin, V. 1826. Explication sommaire des planches d'arachnides de l'Egypte et de la Syrie. Pp. 99–186. *In* Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française, vol. 1(4). C.L.F. Panckoucke: Paris.

Banks, N. 1898. Arachnida from Baja California and other parts of Mexico. Proceedings of the California Academy of Sciences (Zoology) 1: 205–308.

Banks, N. 1902. Papers from the Hopkins Stanford Galapagos Expedition; 1898–1899. VII. Entomological Results (6). Arachnida. With field notes by Robert E. Snodgrass. Proceedings of the Washington Academy of Sciences 4:49–86.

Berland, L. 1927. Note sur les Araignees recueillies aux iles Marquises par le R.P. Simeon Delmas. Bulletin of the Museum of Natural History 38: 366–368.

Berland, L. 1929. Araignées (Araneida), Pp. 35–78. *In* Insects of Samoa and other Samoan terrestrial Arthropoda. British Museum (Natural History), London.

Berland, L. 1933. Araignées des iles Marquises. Bernice P. Bishop Museum Bulletin 114:39–70.

Berland, L. 1934a. Araignées de Polynésie. Annales de la Société Entomologique de France 103:321–336.

Berland, L. 1934b. Les Araignées des Tahiti. Bernice P. Bishop Museum Bulletin 113:97–107.

Berland, L. 1934c. Les Araignees du Pacifique. *In* Contribution a l'étude du peuplement zoologique et botanique des iles du Pacifique. Société de Biogéographie IV (P. Lechevalier, ed.). Lechevalier et fils, Paris.

Berland, L. 1935a. Les Araignées des iles Marquises et la Biogéographie. Compte Rendu Sommaire des Séances de la Société de Biogéographie 100: 27–28.

Berland, L. 1935b. Nouvelle Araignées marquisiennes. Bernice P. Bishop Museum Bulletin 142:31–63.

Berland, L. 1935c. Sur la présence d'espèces Jordaniennes chez les Araignees des certaines iles du Pacifique. Annales de la Société Entomologique de France 103:147–148.

Berland, L. 1938. Liste des Araignees recuellies a Maupiti (Iles de la Societe) par M. Ropiteau. Bulletin de la Société des Etudes Oceaniennes 6: 47–48.

Berland, L. 1942. Polynesian spiders. Occasional Papers of the Bernice P. Bishop Museum 17:1–24.

Bonnet, P. 1959. Bibliographia Araneorum, Pp. 1–5058. Vol. 2(5). Douladoure, Toulouse.

Bryant, E.B. 1945. The Argiopidae of Hispaniola.

Bulletin of the Museum of Comparative Zoology Harvard 95:357–422.

Chamberlin, R.V. 1920. South American Arachnida, chiefly from the Guano Islands of Peru. Brooklyn Museum Science Bulletin 3:35–44.

Chamberlin, R.V. 1924. The spider fauna of the shores and islands of the Gulf of California. Proceedings of the California Academy of Sciences 12:561–694.

Chamberlin, R.V. & W. Ivie. 1942. A hundred new species of American spiders. University of Utah Biological Series 7:1–117.

Chickering, A.M. 1957. The genus *Tetragnatha* (Araneae, Argiopidae) in Panama. Bulletin of the Museum of Comparative Zoology Harvard 116: 301–354.

Chickering, A.M. 1962. The genus *Tetragnatha* (Araneae, Argiopidae) in Jamaica, W. I. Bulletin of the Museum of Comparative Zoology Harvard 127:423–450.

Chrysanthus, F. 1963. Spiders from South New Guinea V. Nova Guinea, Zoology 24:727–750.

Chrysanthus, F. 1975. Further notes on the spiders of New Guinea II (Araneae, Tetragnathidae, Theridiidae). Zoologische Verhandelingen Leiden 140:3–50.

Gertsch, W.J. 1936. Further diagnoses of new American spiders. American Museum Novitates 852:1–27.

Gertsch, W.J. & W. Ivie. 1936. Descriptions of new American spiders. American Museum Novitates 858:1–25.

Gillespie, R.G. 1991. Hawaiian spiders of the genus *Tetragnatha*: I. Spiny leg clade. Journal of Arachnology 19:174–209.

Gravely, F.H. 1921. Some Indian spiders of the subfamily Tetragnathinae. Records of the Indian Museum 22:423–459.

Karsch, E. 1878. Exotisch-araneologisches. Zeitschrift Fur die Gesammten Naturwissenschaften 51:332– 333,771–826.

Koch, L. 1872. *Tetragnatha* Latr., Pp. 170–196 in Die Arachniden Australiens, vol. 1. Bauer and Raspe, Nürnberg.

Levi, H.W. 1981. The American orb-weaver genus *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneidae, Tetragnathinae). Bulletin of the Museum of Comparative Zoology Harvard 149:271–318.

Marples, B.J. 1957. Spiders from some Pacific Islands, II. Pacific Science 11:386–395.

Meyrick, E. 1935. Pyrales and Microlepidoptera of the Marquesas Islands. Bernice P. Bishop Museum. Bulletin. 114:333–355.

Okuma, C. 1968. Two spiders new to fauna of Japan. Acta Arachnologica 21:40–42.

Okuma, C. 1980. Notes on a spider *Tetragnatha laqueata* L. Koch, 1871 of the Bonin Islands, Japan (Araneae: Tetragnathidae). Esakia 15:75–78.

Okuma, C. 1983. New synonomies and new records of some cosmopolitan species of the genus *Tetragnatha* (Araneae; Tetragnathidae). Esakia 20: 69–80.

Okuma, C. 1987. A revision of the Australasian species of the genus *Tetragnatha* (Araneae, Tetragnathidae). Esakia 25:37–96.

Platnick, N.I. 1997. Advances in Spider Taxonomy 1992–1995, with redescriptions 1940–1980. New York Entomological Society in association with the American Museum of Natural History, New York.

Rainbow, W.J. 1920. Arachnida from Lord Howe and Norfolk Islands. Records of the South Australian Museum 1:229–272.

Roewer, C. 1942. Katalog der Araneae von 1758 bis 1940. R. Friedländer und Sons: Bremen.

Seeley, R.M. 1928. Revision of the spider genus *Tetragnatha*. Bulletin of the New York State Museum 278:99–150.

Simon, E. 1890. Études arachnologiques, 22e memoires. Annales de la Société Entomologique de France (6) 10:131–136.

Simon, E. 1897. On the spiders of the island of St Vincent. III. Proceedings of the Zoological Society London 65:860–890.

Strand, E. 1911. Araneae von den Aru- und Kei-Inseln. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 34:129–199.

Taczanowski, L. 1878. Les Aranéides du Pérou central. Horae Societatis Entomologicae Rossicae 14:140–175.

Thorell, T. 1890. Studi sui ragni Ragni Malesi e Papuani, I. Annali del Museo Civico di Storia Naturale di Genova 8.

Thorell, T. 1895. Descriptive Catalogue of the Spiders of Burma. British Museum (Natural History), London.

Walckenaer, C.A. 1837. Histoire naturelle des Insectes. Aptères, Pp. 203–226. Vol. II. Librairie Encyclopédique de Roret, Paris.

Yaginuma, T. 1979. Spiders of the Bonin islands, Japan. Nature and Animals (Japan) 9:33–36.

Manuscript received 28 September 2001, revised 19 April 2002.

2003. The Journal of Arachnology 31:173–208

PHYLOGENETIC ANALYSIS OF *SANTINEZIA* WITH DESCRIPTION OF FIVE NEW SPECIES (OPILIONES, LANIATORES, CRANAIDAE)

Ricardo Pinto-da-Rocha: Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, n. 321, 05508–900, São Paulo, SP, Brazil. E-mail: ricrocha@usp.br

Adriano B. Kury: Departamento de Invertebrados, Museu Nacional, Quinta da Boa Vista, São Cristóvão, 20.940-040, Rio de Janeiro, RJ, Brazil

ABSTRACT. The taxonomic status of all species of *Santinezia* Roewer 1923 is defined, and a catalogue is provided. *Santinezia lucifer*, *S. gracilis*, *S. onorei* (all from Ecuador), *S. furva* (from Colombia and Venezuela) and *S. hermosa* (from Peru) are newly described. *Santinezia biordi* González-Sponga 1991 is newly considered as a junior subjective synonym of *S. serratotibialis* Roewer 1932. *Santinezia albilineata* Roewer 1932, *Goniosoma pavani* Muñoz-Cuevas 1972, *S. benedictoi* Soares & Avram 1981, *S. decui* Avram 1987, *S. orghidani* Avram 1987 and *S. francourbani* Avram 1987 are newly considered as junior subjective synonyms of *Inezia curvipes* Roewer 1916. *Nieblia* Roewer 1925, *Chondrocranaus* Roewer 1932, *Macuchicola* Mello-Leitão 1943 and *Carvalholeptes* H. Soares 1970 are newly considered as junior subjective synonyms of *Santinezia*. *Nieblia camposi* Mello-Leitão 1942 is transferred to *Spinicranaus* Roewer 1913. *Santinezia albimedialis* Goodnight & Goodnight 1943 is transferred to *Phareicranaus* Roewer 1913. *Nieblia magna* Roewer 1932 is transferred to *Neocranaus* Roewer 1913. *Santinezia micheneri* Goodnight & Goodnight 1947 is newly considered as a junior subjective synonym of *Phareicranaus ornatus* Roewer 1932. A character survey is done including newly discovered characters of genital morphology, patterns of colored marks of dorsal scutum and armature of male leg IV. A phylogenetic analysis of the species of the genus for which males are known is provided allowing the definition of three new species groups. Comparative descriptions are given of the penial morphology of one species of *Ventrivomer*, one species of *Phareicranaus* and eight species of *Santinezia*. Distribution maps for all species of *Santinezia* are given. The type locality of *S. serratotibialis* Roewer 1932 is corrected from Trinidad (Bolivia) to Trinidad (Trinidad & Tobago).

Keywords: Laniatores, Neotropics, harvestmen, phalangids, taxonomy

Following a general trend of multiplication of families in the opilionid suborder Laniatores recognizing phylogenetic patterns, the immense neotropical family Gonyleptidae as defined by Roewer (1913, 1923) was gradually dismembered by subsequent authors. Mello-Leitão (1935, 1949) removed six subfamilies to constitute the Stygnidae. Kury (1994) removed another four subfamilies to form the Cranaidae, and Kury (1997) later elevated the Manaosbiinae to familial status. Even after this major distilling, the Gonyleptidae is still the largest family of the Laniatores, with more than 800 valid species.

The family Cranaidae encompasses 170 species distributed exclusively in South America, along the Andes and Amazon Basin up to Panama and Venezuela. The cranaids are members of the Gonyleptoidea that do not possess a dorsal process on the glans penis, except for the basalmost genera such as *Prostygnus* and *Cutervolus*, which also lack a ventral process. Sexual dimorphism may be present in the carapace (larger in males), the cheliceral hand (swollen in males), spines and apophyses of coxa to tibia IV (larger in males). However, cranaids never have a gonyleptid-like sinuous branched apophysis in coxa IV. Spines of eye mound, areas I–III and free tergites when present are very high and sharp. The traditional (e. g., Roewer 1923) generic divisions within Cranaidae are unsatisfactory, with a high number of monotypic genera. These genera are defined by characters deemed to be of "generic value", whatever that is intended to mean. Such characters are

usually sexually dimorphic, variable, of unclear definition, or meaningless, and a positive generic identification is often a matter of chance.

The genus *Inezia* was described by Roewer (1913) for a single species from Ecuador. Later, Roewer (1915, 1916) added three more species from Colombia and Venezuela. The name *Inezia* was preoccupied and Roewer (1923) proposed the replacement name *Santinezia*. Over the years, various authors described more species from northern South America, making it the most species-rich genus in the Cranaidae, with a high degree of endemism. However, *Santinezia*'s relationship with other genera is unclear, and some species are barely, if at all, recognizable. The poor state of Laniatorean systematics even caused a typical *Santinezia* to be described by Muñoz-Cuevas (1972) as a *Goniosoma*, a genus of Gonyleptidae. It is interesting to note that *Santinezia* and *Goniosoma* show a high level of convergence, each presumably occupying the same niche respectively in the Andes and lowland forests of Amazonia and in the Brazilian Atlantic Forest (called domain of *Mata Atlântica* in Portuguese by Ab'Saber [1977]). Only details of leg armature and the male genitalia betray their remote common ancestry. Both are very large Gonyleptoidea with glossy teguments, stout and long legs that are weakly armed, robust and heavily armed pedipalps, and area II projecting into area I until it touches the scutal groove.

Our examination of many *Santinezia* species mainly from Ecuador and Peru created the opportunity to revise this genus. *Santinezia* is here given a phylogenetic definition and the relationships among its species are assessed through cladistic analysis. We provide a key, maps and diagnoses for species and species groups. In the diagnoses given below, putative apomorphies are preceded by (A) and plesiomorphies are preceded by (P). Nomenclature of cheliceral segments is: basichelicerite = segment I = trochanter; hand = segment II, including basis of chela and fixed finger; movable finger = segment III. Notation of tarsal segmentation as in Avram (1973), notation of pedipalpal spination as in Mello-Leitão (1939). We did not deem it necessary to examine some type specimens from European museums. Transport across continents can be slow and hazardous and in view of the present policy of protection of fauna we only do that in a small number of cases. In most instances, however, original descriptions are enough to recognize with certainty a given species.

All the specimens examined were preserved in ethanol and the description of color was based on this material. The external structures were studied under a stereomicroscope at magnifications between 10× & 80×. Tubercles are tegumentary processes with a blunt apex as wide as long. Spines are tegumentary processes at least two times longer than wide, usually with a sharp point. In *Santinezia*, spines are located on the eye mound, area III and free tergites. The diagnosis of each species is given comparatively within each group of species.

Acronyms of repositories are: American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS); private collection of Helia E. M. Soares (HSPC), now transferred to MNRJ; Institutul de Speologie "Emile Racovitza", Bucarest (ISER); private collection of Miguel A. González-Sponga, Caracas (MAGS); Museo de Biología de la Sociedad Venezolana de Espelología, Caracas (MBSVE); Museo de Biología de la Universidad de Zulia, Maracaibo (MBUZ); Museo de Ciencias Naturales de Caracas, Caracas (MCNC); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima (MUSM); Museo di Zoologia della Università di Torino, Torino (MZT); Museu de Zoologia, Universidade de São Paulo, São Paulo (MZSP); Swedish Museum of Natural History, Stockholm (NRMS); Pontificia Universidad Catolica de Quito, Quito (PUCQ); Senckenberg Museum, Frankfurt am Main (SMF); National Museum of Natural History, Washington DC (USNM); and Zoologisches Museum der Humboldt Universität, Berlin (ZMB).

PHYLOGENETIC ANALYSIS

Outgroup choice.—Following the protocol delineated by Nixon & Carpenter (1993), no previous assumptions about polarity were made. Using different prime outgroups to root the trees has proven to yield different results. Two cranaid genera which have male genitalia

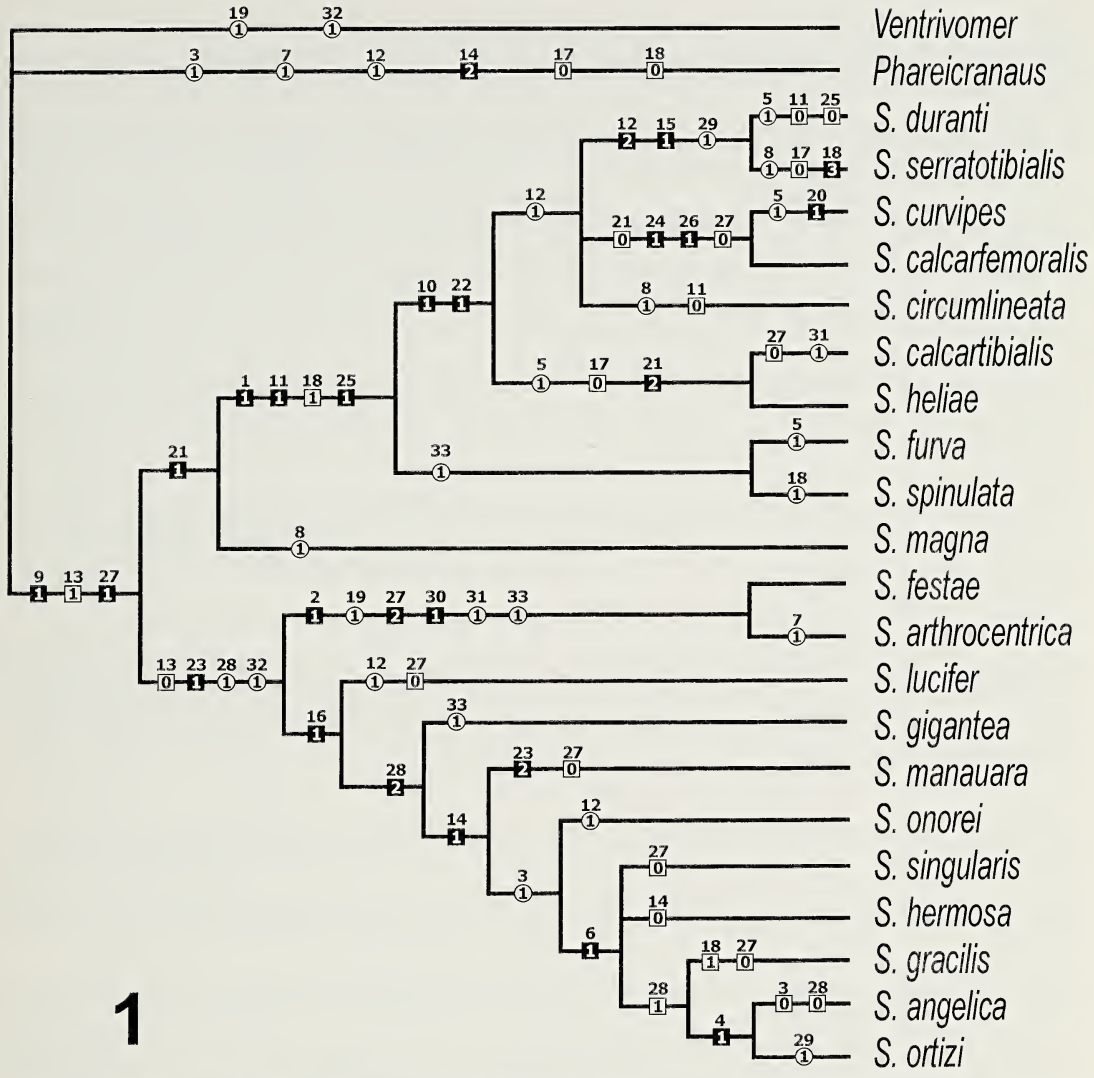


Figure 1.—Cladogram showing proposed hypothesis of relationships for the species and species groups of *Santinezia*. This tree is the output by Pee-Wee, and has a fit of 168.9. Statistics by CLADOS under equal weights are: length = 80, CI = 53 and RI = 72.

and leg armature similar to *Santinezia*, *Phareicranaus* Roewer 1913 and *Ventrivomer* Roewer 1913, were used as outgroups. To represent these genera we used the species *Phareicranaus ornatus* (Roewer 1932), which was once described as a *Santinezia*, and *Ventrivomer ancyrophorus* (Butler 1873).

Ingroup terminals.—Only the species in which males are known were included in the analysis. The type species of *Carvalholeptes* H. Soares 1970, *Macuchicola* Mello-Leitão 1943 and *Nieblia* Roewer 1925 were also included since they all fit in the monophyletic *Santinezia* as perceived by us.

Characters.—A character survey was done without regard to preconceptions regarding the characters being of value for "generic" or "specific" separations. In total, 34 characters were studied, 17 regarding armature of male pedipalp and/or leg IV, nine regarding male genitalia and eight regarding armature and color patterns of the dorsal scutum (see Tables 1 & 2). Thus, more than three-fourths (26 out of 34 characters) required information strictly obtained from males. This is why species of which only females are known were omitted from the analysis.

Methods of analyses.—We studied the re-

Table 1.—Annotated list of the 34 characters surveyed for the phylogenetic analysis of *Santinezia*. The plesiomorphic (P) state is indicated as zero (0), apomorphic (A) states as (1) and (2).

A. Scutum.

1) Size of paramedian spines of scutal area III: (0) stout, (1) small (less than height of eye mound).
2) Size of paramedian spines of scutal area I: (0) absent or minute, (1) high and sharp, as exemplified in *S. arthrocentrica* (Fig. 38).
3) Spines of eye mound and free tergites: (0) concolor with body background, (1) contrasting yellow.
4) Spines of area III: (0) concolor with body background, (1) black, sharp contrasting.
5) Grooves I–III: (0) without stripe, (1) each with thin white stripe all over its boundary, as exemplified in *S. furva* (Fig. 41).
6) Dorsal surface of scutum: (0) without circular spots, (1) with variable pattern of small circular white spots, as exemplified in *S. gracilis* (Fig. 8).
7) Cross-like white drawing on mesotergum: (0) absent, (1) present as in some *Phareicranaus*.
8) White stripes on anterior part of lateral areas, on posterior margin of scutum and posterior margin of free tergite III: (0) absent, (1) present.

B. Penis.

9) Inflatable sac of glans penis: (0) irregularly folded (Figs. 2–5), (1) with many similar thin folds arranged in a stack (Figs. 6, 7, 11, 12). The latter is a putative autapomorphy of *Santinezia*.
10) Distal group of setae of ventral plate: (0) including 3–4 common setae (Figs. 6, 12), (1) including only one spatulate seta (Fig. 46).
11) Basal group of setae of ventral plate: (0) three, rarely two, forming nearly longitudinal row (Figs. 7, 33), (1) five, forming two nearly transverse rows (Fig. 47).
12) Intersetal portion of ventral plate lateral border: (0) short (0.25 of most basal seta to most distal), (1) medium (0.35 of most basal seta to most distal), (2) long (0.70 of most basal seta to most distal).
13) General shape of ventral plate: (0) roughly rectangular, (1) shaped like the body of a guitar, with a constriction in the middle (Fig. 45), (2) roughly square (Fig. 2).
14) Distal margin of ventral plate: (0) entire (Fig. 2), (1) with shallow cleft (Fig. 33), (2) with deep cleft (Fig. 5).
15) Stylar tip: (0) continued as a soft bent lobe (Figs. 33, 34), (1) ending sharply without soft part (Figs. 46, 47).
16) Stylar subdistal pointed apophysis: (0) absent (Figs. 23, 34), (1) present (Fig. 45).
17) Dorsal process of glans (projection digitiform in front of the stylus): (0) present (Fig. 4), (1) absent.

C. Coxa of leg IV of males.

18) Ventral apophysis of coxa IV of male: (0) absent, (1) short, twice longer than wide, (2) stout, more than five times longer than wide.
19) Position of ventral apophysis of coxa IV of male: (0) on the posterior border of coxa, near stigmata (Fig. 16), (1) far from stigmata, located in the middle of coxa (Fig. 38).
20) Orientation of apophysis of coxa IV of male: (0) erect, (1) oblique backwards as in *S. curvipes*

D. Tibia of leg iv of males.

21) Mesal row of spines of tibia IV of male: (0) without this row (1) with mesal row of 8–12 oblique spines occupying proximal half pointed backwards with size decreasing apically, as in *S. serratotibialis*, (2) this row displaced distally, as in *S. heliae*.
22) First spine of basal row in male tibia IV: (0) straight (as in *S. magna*), (1) geniculate (as exemplified in *S. serratotibialis*).
23) Ventral mesal spines of tibia IV of male: (0) absent, (1) with two-three ventral mesal short spines in basal fourth, the most proximal hook-shaped curved proximally (as in *S. angelica, S. hermosa* and *S. singularis*), (2) only one more distal in mid length.

E. Femur of leg IV of males.

24) Basal portion of femur IV of male: (0) straight (Fig. 10), (1) curved (see Roewer, 1923: fig. 692).
25) Accessory ecto-apical spines of femur IV of male: (0) without, (1) with 3–7 very small clustered spines, apical to the main spine, as in *S. serratotibialis*.
26) Sub-apical mesal apophysis of femur IV of male: (0) absent, (1) apophysis present (not ventral) stout, almost transverse and strongly curved (hooked) anteriorly as in *S. curvipes* (See Roewer, 1923: fig. 692).

Table 1.—Continued

27) Sub-apical-ectal apophysis of femur IV of male: (0) without, (1) with stout curved apophysis (Fig. 15), (2) with two slightly smaller accessory apophyses (Fig. 37).
28) Submedial mesal apophysis of femur IV of male: (0) without, (1) with two or three short apophyses (Fig. 10), (2) with only one submedial mesal stout apophysis curved proximally (as exemplified in *S. manauara, S. singularis* and *S. gigantea*) (Fig. 31).
29) Sub-basal ventro-mesal apophysis of femur IV of male: (0) without, (1) with straight apophysis as in *S. serratotibialis.*
30) Ectal and mesal row of spines of femur IV of male: (0) absent (surface at most finely granular), (1) with row of subequal spines as in *Nieblia festae* and *Macuchicola arthrocentrica* (Fig. 37).

F. Other.

31) Trochanter III of male: (0) unarmed, (1) with stout spiniform basal inner apophysis.

G. Femur of pedipalp.

32) Shape of femur of pedipalp of male: (0) incrassate, strongly convex dorsally, (1) cylindrical as in *S. hermosa.*
33) Meso-apical seta of femur of pedipalp: (0) without, (1) with stout seta (Fig. 36).
34) Dorso-apical spine of femur of pedipalp: (0) without, (1) with stout spine (smaller in *S. curvipes* and *S. serratotibialis*) (Figs. 16, 32, 38).

lationships of the species with parsimony analysis, using the computer programs Hennig86 version 1.5 (Farris 1988) and Pee-Wee version 1.96 (Goloboff 1993a, 1993b). All characters were considered to be unordered. For Hennig86 we used the option implicit enumeration (ie), which provides an exact solution. In Pee-Wee, parsimony favors maximal

Table 2.—Distribution of the character states among the terminal taxa for the analysis of species of *Santinezia,* including the outgroups *Ventrivomer* and *Phareicranaus.* ? = state unknown; – = not applicable for this character.

	0	1	2	3
Character numbers:	1234567890123456789012345678901234			
Ventrivomer	00000000000020001210000000000000100			
Phareicarnaus	00100010000122000--0-000000000001			
S. singularis	00100100100001011200 0-10-002000101			
S. angelica	00010100??????????2??0-10001000?01			
S. gigantea	00000000100000011200 0-10001200011 1			
S. gracilis	00100100100001011100 0-10-001000101			
S. hermosa	00100100100000011200 0-10001200010 1			
S. lucifer	00000000100100011200 0-10-001000101			
S. manauara	00000000100001011200 0-20-002000101			
S. onorei	00100000100101011200 0-10001200010 1			
S. ortizi	00110100??????????2000-?00011100101			
S. arthrocentrica	01000010100000001210 0-10002101111 1			
S. festae	01000000??????????2100-10002101 1?11			
S. calcafemoralis	10000000??????????1000-01-100000?01			
S. calcartibialis	10001000????????????2100-000001?01			
S. circumlineata	10000001110110001 1?011001010000001			
S. curvipes	10001000111110001 1010-01-100000001			
S. duranti	10001000110210101 1?011000010100001			
S. furva	10001000101010001 1001000101000001 1			
S. heliae	10001000111010000 1?021001010000001			
S. magna	?0000001?????????2??10000010002??1			
S. serratotibialis	10000001111210100 3?011001010100001			
S. spinulata	?0000000??????????2??10001010002011			

fit trees instead of minimal length trees. This package allows greater resolution than similar programs, even with incomplete matrices. With Pee-Wee the concavity values 1, 3 and 6 were tried. Algorithms used were "search, max, mult, jump" and "nelsen". Output was then studied with CLADOS (Nixon 1992).

Results of analysis.—Pee-Wee produced 50 optimal trees of maximal fit 252.0. The fully resolved strict consensus tree (obtained with the nelsen algorithm) was analyzed by CLADOS (under equally weighted characters), and the statistics obtained were length = 80, CI = 53 and RI = 72. The cladogram is shown in Fig. 1.

Given the outgroups used, the monophyly of *Santinezia* is well supported by the inflatable sac of glans penis with thin folds (character 9, state 1), ventral plate of penis guitar-shaped (character 13-1) and curved apophysis on male femur IV (character 27-1).

The results of cladistic analysis permitted us to propose three species-groups: group curvipes with the synapomorphic character 21(1), 8–12 oblique spines on proximal half of male tibia IV; group festae based on (character 2-1), ventral apophysis of male coxa IV located on middle region (character 19-1), sub-apical-ectal male femur IV with two slightly smaller accessory apophyses (character 27-2), subequal spines on ectal and mesal male femur IV (character 30-1), stout basal inner apophysis on male trochanter III (character 31-1) and stout meso-apical seta on femur pedipalp (character 33-1); and group gigantea based on presence of stylar subdistal pointed apophysis (character 16-1).

TAXONOMY

Family Cranaidae Roewer 1913

Neocranaus Roewer 1913

Neocranaus Roewer 1913: 408; Roewer 1923: 561; Roewer 1932: 282; Mello-Leitão 1935: 96; Soares & Soares 1948: 609 [= *Belemicola* Roewer 1932] (type species *Neocranaus albiconspersus* Roewer 1913, by monotypy).

Acanthocranaus Roewer 1913: 411; Roewer 1923: 562; Roewer 1932: 282 (type species *Acanthocranaus calcariger* Roewer 1913, by monotypy). Synonymy established by Soares & Soares (1948).

Diagnosis.—Cranainae with stigmatic area and coxa IV ventrally unarmed in both sexes. Pedipalpal femur without dorso apical spine. Eye mound and scutal area III with a pair of high spines. Tarsal counts 7/11–12/7/7. Closest to *Paracranaus* judging by details of the armature, shape of legs and pedipalps. Distinguished from all other cranaines by the lanceolate granular area extending from carapace to area III and the clusters of white sharply contrasting tubercles on lateral area.

Included species.—*Neocranaus albiconspersus* Roewer 1913 and *N. magnus* (Roewer 1932).

Remarks.—Soares & Soares (1948) synoynymized *Acanthocranaus* with *Neocranaus*, but this synonymy was not based on examination of any material or in any argumentation other than matching the Roewerian grid. We feel that the type species of both genera do not share important characters of pedipalpal spination, but it is beyond the scope of this paper to review the generic validity of cranaid species. To revalidate *Acanthocranaus* without reviewing the genera and without knowledge of the genital morphology is futile at this stage. *Nieblia magna* clearly does not belong to *Santinezia*. *Neocranaus* has not been included as outgroup in the analysis.

Neocranaus magnus (Roewer 1932), new combination

Nieblia magna Roewer 1932: 349, fig. 66; Soares & Soares 1948: 611 (type SMF RII 1453/64, female holotype, not examined).

Type locality.—PANAMA.

Remarks.—The type species of *Nieblia* is synonymized with *Santinezia* in this study. The information available on *Nieblia magna* is only based on the original description of a female. This species is tentatively transferred to *Neocranaus* Roewer, 1913 based on the larger ectal and dorso-mesal tubercles on trocanther IV, dorsal apex of femur of pedipalp with a stout spine, meso-apical seta on pedipalp femur and armature of eye mound, areas I–III and free tergites. Those features are present in *Acanthocranaus calcariger* but not in *Neocranaus albiconspersus*.

Phareicranaus Roewer 1913

Phareicranaus Roewer 1913; Soares & Soares 1948: 612; Roewer 1952: 56 (type species *Goniosoma calcariferum* Simon 1879).

Diagnosis.—Cranainae with ventral plate deeply cleft in distal border. With four groups of setae. Glans with dorsal process. Stylus

smooth, slightly curved, without stylar apophysis. Apex bent in obtuse angle, forming a deeply depressed tongue-shaped lobe. Stigmatic area and coxa IV ventrally unarmed in both sexes. Pedipalpal femur with dorso apical spine. Eye mound and scutal area III with a pair of high spines. Tarsal counts 7–8/15/8–9/10. Closest to *Santinezia* by the scute outline, genitalic features and large body and leg size, distinguished mainly by the absence of ventral armature in coxa IV.

Included species.—*Phareicranaus albigranulatus* Roewer 1913, *P. albigyratus* Roewer 1932, *P. albimedialis* (Goodnight & Goodnight 1943), *P. calcariferus* (Simon 1879), *P. camposi* (Mello-Leitão 1942), *P. cingulatus* Roewer 1932, *P. festae* Roewer 1925, *P. giganteus* Roewer 1932, *P. magnus* (Roewer 1932), *P. ornatus* Roewer 1932, *P. parallelus* Roewer 1925 and *P. x-albus* Roewer 1925.

Phareicranaus albimedialis (Goodnight & Goodnight 1943), new combination

Santinezia albimedialis Goodnight & Goodnight 1943: 8, figs. 23–25; Soares & Soares 1948: 617 (type AMNH female holotype and female paratypes, examined).

Phareicranaus bolivarius Roewer 1952: 56, fig. 21 (types SMF 9804/83 male holotype 2 female paratypes;, Weyrauch 3 females, 1 juvenile paratypes, not examined). NEW SYNONYMY.

Type localities.—Of *S. albimedialis*: PERU. Of *P. bolivarius*: PERU: *San Martín:* Rio Huallaga, tropical rain forest: Juanjui, 350 m.

Records.—PERU: *San Martín:* Rio Huallaga, tropical rain forest: Saposoa, 420 m (Roewer 1952).

Remarks.—Roewer (1952) raised the possibility that *P. bolivarius* was synonymous with *S. albimedialis*, but he seemed to be bound by his own taxonomic paradigm. The type series of *S. albimedialis* has been examined and compared to Roewer's descriptions of both species. We could not find any meaningful difference between the two alleged species, which agree in every characteristic. *Santinezia* and *Phareicranaus* can only be distinguished by examining male specimens. The type series of the species described by Goodnight & Goodnight (1943) contained only females, making the generic placement impossible. Roewer examined males and females and correctly placed his species in *Phareicranaus*.

Phareicranaus ornatus Roewer 1932 (Figs. 4–5)

Phareicranaus ornatus Roewer 1932: 302, fig. 18; Soares & Soares 1948: 614 (type SMF RII 2597/68, female holotype, not examined).

Santinezia micheneri Goodnight & Goodnight 1947: 11, figs. 31–33 (types AMNH, male holotype, not examined, 1 male paratype, examined). NEW SYNONYMY.

Type locality.—Of *P. ornatus*: COSTA RICA. Of *S. micheneri*: PANAMA.

Material examined.—Paratype: 1 male paratype of *S. micheneri*, El Valle de Anton, 22 December 1945, C.D. Michener (HSPC-983).

Other material.—PANAMA. *Coclé:* 1 ♂, 1 ♀, La Mesa above El Valle, 1200 m, 30 January 1987, E.S. Ross (CAS).

Supplementary description.—*Male genitalia* (Figs. 4–5). Ventral plate oblique in relation to truncus axis, subrectangular, deeply cleft in distal border. With four groups of setae: two straight latero-basal, one slightly curved latero-distal, one short curved dorsolateral distal, two curved latero-apical. Glans with well-developed dorsal process, as thick as base of stylus. Stylus smooth, slightly curved. Apex bent in obtuse angle, forming a deeply depressed tongue-shaped lobe with a few ridges and without noticeable papillae and processes. Without stylar apophysis.

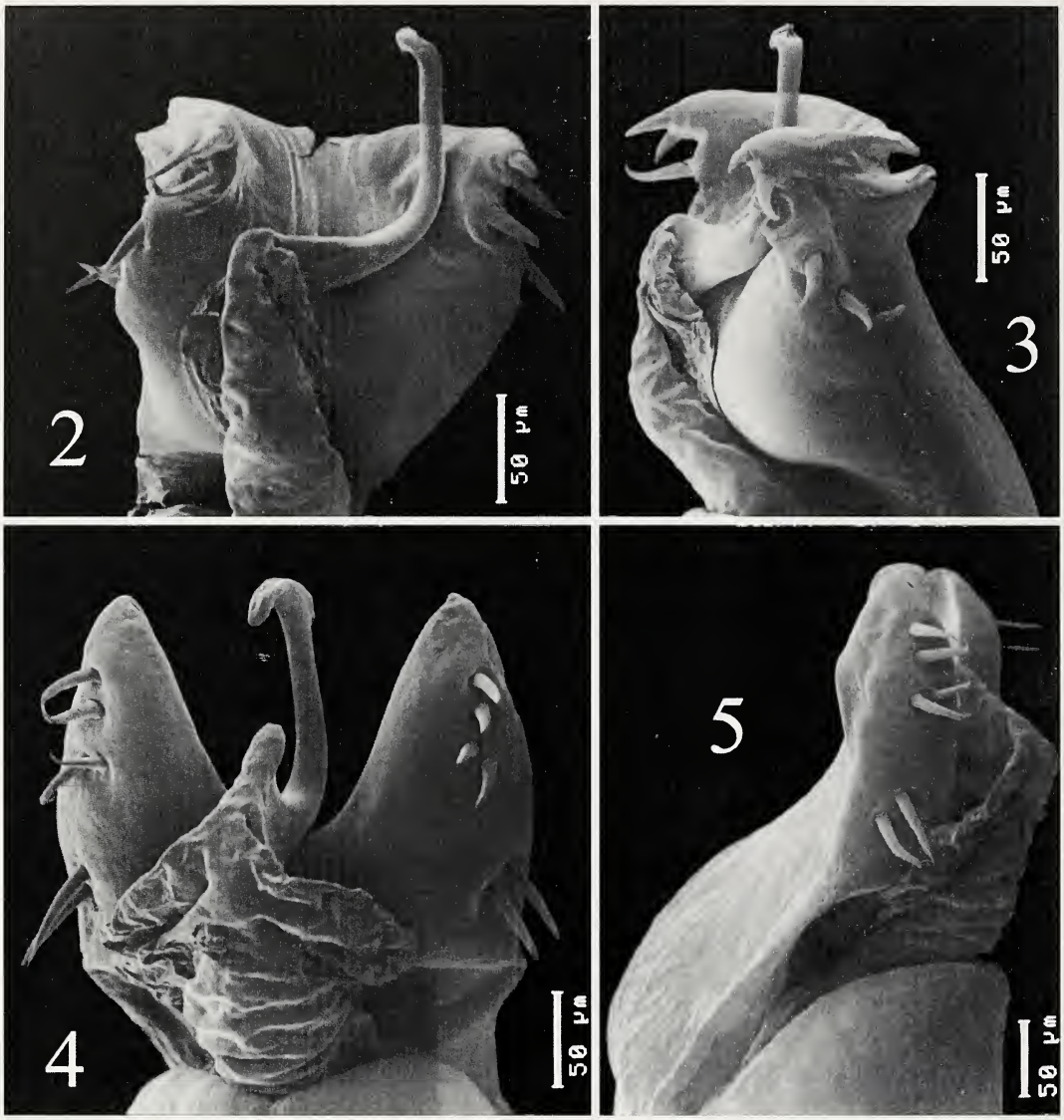
Spinicranaus Roewer 1913

Spinicranaus Roewer, 1913: 414 (type species *Cranaus diabolicus* Simon 1879, by monotypy).

Diagnosis.—Cranainae with a pair of high spines on the eye mound, mesotergal areas I and III. Granulations clustered on carapace behind eye mound, around spines of area I, as single transverse row in area II and around spines of area III. Pedipalpal femur with dorso apical spine. Tarsal counts 7/?/9/10. Distinguished from all other cranaines by the strong dorsal apophysis of cheliceral bulla and the extremely strong spines on frontal border of carapace.

Remarks.—*Spinicranaus* has not been included as outgroup in the analysis.

Included species.—*Spinicranaus camposi* (Mello-Leitão 1942); *S. diabolicus* (Simon 1879)



Figures 2–5.—Male genitalia of two species of Cranainae, distal part of penis: 2–3. *Ventrivomer ancyrophorus* (Butler 1873) male (PUCQ). 2. Dorsal view; 3. Same, lateral view. Figures 4–5. *Phareicranaus ornatus* (Roewer 1932) male (HSPC-983): 4. Dorsal view; 5. Same, lateral view. Scale bars = 0.05 mm.

Spinicranaus camposi (Mello-Leitão 1942) new combination

Nieblia camposi Mello-Leitão 1942: 322, fig. 9; Soares & Soares 1948: 611 (type MNRJ female holotype, type lost, not examined).

Remarks.—*Nieblia camposi* shares with *C. diabolicus* the same granulation pattern as described above, on the other hand there is no positive evidence to relate it to *Santinezia*.

Type locality.—ECUADOR: *Zamora-Chinchipe:* Zamora (04°04′S, 78°58′W).

Ventrivomer Roewer 1913

Ventrivomer Roewer 1913: 380; Roewer 1923: 546; Mello-Leitão 1926: 363; Roewer 1932: 289; Soares & Soares 1948: 621; H. Soares 1970: 330 (type species *Gonyleptes ancyrophorus* Butler 1873, by monotypy).

Included species.—Only the type species.

Diagnosis.—Cranainae with ventral plate entire with three basal and three distal setae, those arising in the distal margin of the plate; glans without dorsal or ventral processes; sty-

lus strongly bent in straight angle with ornamented apex and without stilar apophysis. Stigmatic area in males bearing a huge process bifid in the apex. Pedipalpal femur without dorso apical spine. Eye mound and scutal area III with a pair of high spines. Coxa IV of male ventrally with two stout spines. Tarsal counts 7/10/9/10. Compared to *Ventrifurca* Roewer 1913 and other genera with huge bifurcate hook in posterior border of stigmatic area. Promptly distinguished from all of them by the absence of ventral armature in coxa IV.

Ventrivomer ancyrophorus (Butler 1873)
(Figs. 2, 3)

Gonyleptes ancyrophorus Butler 1873: 116, pl. 3, figs. 5–6 (type BMNH, male holotype, not examined).

Ventrivomer ancyrophorus: Roewer 1913: 380, fig. 148; Roewer 1923: 547, fig. 682; Roewer 1932: 289; Soares & Soares 1948: 621.

Type locality.—ECUADOR: *Pichincha:* Quito.

Other records.—ECUADOR: Gualia (Roewer 1923). BOLIVIA: *Beni:* Trinidad (Roewer 1932).

Material examined.—ECUADOR: *Pichincha:* 1 ♂, neighborhood of Quito, 26 January 1985, S.N. Paz (PUCQ).

Supplementary description.—*Male genitalia* (Figs. 2, 3)*:* Ventral plate oblique in relation to truncus axis, trapezoid, not cleft at distal border. Dorsally concave, with strong distal fold forming a ventrodistal gutter. With three groups of short curved subequal setae: two latero-basal, one latero-distal and three dorso-lateral distal. Glans without dorsal process. Stylus smooth, bending in straight angle in the half-length. Apex bent in acute angle, not depressed nor swollen, with apical papillae, without stylar apophysis.

Santinezia Roewer 1923

Inezia Roewer 1913: 392 [preoccupied by *Inezia* Cherrie 1909]; Mello-Leitão 1926: 39; Mello-Leitão 1932: 113 (type species *Inezia gigantea* Roewer 1913, by monotypy).

Santinezia Roewer 1923: 552 [replacement name]; Mello-Leitão 1932: 122; Roewer 1932: 289; Mello-Leitão 1935: 96; Kästner 1937: 389; Soares & Soares 1948: 616; Roewer 1963: 69; González-Sponga 1989: 59 (type species *Inezia gigantea* Roewer 1913).

Nieblia Roewer 1925: 27; Roewer 1932: 348; Soares & Soares 1948: 610 (type species *Nieblia festae* Roewer 1925). NEW SYNONYMY.

Chondrocranaus Roewer 1932: 341; Soares & Soares 1948: 592 (type species *Chondrocranaus scriptus* Roewer 1932, by monotypy). NEW SYNONYMY.

Macuchicola Mello-Leitão 1943: 4; Soares & Soares 1948: 606 (type species *Macuchicola arthrocentrica* Mello-Leitão 1943, by original designation). NEW SYNONYMY.

Carvalholeptes H. Soares 1970: 330 (type species *Carvalholeptes singularis* H. Soares 1970, by original designation). NEW SYNONYMY.

Diagnosis.—Cranaidae with eye mound and area III with pair of high spines; free tergite I unarmed, II–III with pair of spines. Pedipalpal femur of male with dorso apical spine; coxa IV of male with pair of spiniform ventral apophyses near stigmata and dorso apical small spine. Stigmatic area unarmed. Glans without or with very small dorsal process. Stylus may bear spiniform stylar apophysis; ventral plate variable, never deeply incised distally. Tarsal counts 7–10/13–23/8–12/9–14. Distinguished from *Phareicranaus* by coxa IV of male ventrally armed. From *Ventrivomer* by absence of ventral bifurcate hook in stigmatic area. From *Spinicranaus* by cheliceral bulla smooth and frontal border of carapace unarmed. From *Neocranaus* by pedipalpal femur with dorso-apical spine and scutum without piriform granular area.

Remarks.—The grounds for the erection of different genera by Roewer, Mello-Leitão and Soares are in our view feable and do not hold up under closer scrutiny (see Table 3). Mello-Leitão (1943), in the diagnosis of *Macuchicola*, stated that "the armature of coxa IV is entirely original, which lets one promptly recognize this striking genus". It is not known if he was referring to the plain presence of two ventral spines on the coxae IV, a feature already recorded for other genera (such as *Santinezia* and *Ventrivomer*), or to the more anterior placement of the spines, which was described 18 years before for *Nieblia*. H. Soares (1970), in the description of *Carvalholeptes*, stated that it possessed a pair of spines in the stigmatic area, comparing it to *Ventrivomer*. But even her drawing of the male in ventral view shows that the spines are clearly located in the coxae as in all other *Santinezia*. Our examination of the type material

Table 3.—Summary of the diagnostic Roewerian characters used in the literature to support the genera in which the species of *Santinezia* have been included (Roewer 1913; Roewer 1943; Mello-Leitão 1943; H. Soares 1970); "vv"= pair of spines, "oo" = pair of tubercles; "—" = unarmed.

Genus	Meso-tergal area I	Meso-tergal area III	Apophysis on body venter	Tergite I	Tergite II	Tergite III
Santinezia	oo	vv	in coxa IV	— or vv	vv	vv
Nieblia	vv	vv	in coxa IV	—	vv	vv
Phareicarnaus	oo	vv	absent in both sexes	—	vv	vv
Macuchicola	vv	vv	in coxa IV, more frontal	—	vv	vv
Carvalholeptes	—	vv	in "stigmatic area"	—	vv	vv
Chodrocranaus	oo	vv	only females	vv	vv	—

of *Carvalholeptes singularis* confirmed this suspicion.

Included species groups.—Group gigantea, group festae and group curvipes.

Santinezia gigantea species group

Diagnosis.—Paramedian spines of scutal area III very high (character 1, state 0) [P]. Paramedian spines of scutal area I absent or minute (character 2, state 0) [P]. Basal group of setae of ventral plate three, rarely two, forming nearly longitudinal row (character 11, state 0) [P]. General shape of ventral plate roughly rectangular (character 13, state 0) [P]. Ventral apophysis of coxa IV located on the posterior border of coxa, near stigmata (character 19, state 0) [P]. Tibia IV of male without mesal row of spines occupying proximal half (character 21, state 0) [P]. Tibia IV of male without two-three ventro-mesal short spines in basal fourth, the most proximal hook-shaped curved (character 23, state 1) [P]. Femur IV of male without accessory spines ecto-apical (character 25, state 0) [P]. Femur IV of male: (0) without or with stout curved sub apical ectal apophysis and no accessory apophyses. (character 27, states 0–1) [P]. Femur IV of male with or without submedial mesal apophyses (character 28, states 1–3) [P-A]. Femur IV of male ectal and mesal at most finely granular (character 30, state 0) [P]. Pedipalpal femur of male cylindrical (character 32, state 1) [A]. Distinguised from the group *festae* by the posterior position of ventral spines in coxa IV. From group *curvipes* by the armature if leg IV in male, presence in some species of a pattern of white circles, no white stripes, and in general dark body background color.

Included species.—*Santinezia angelica* Roewer 1963, *S. gigantea* (Roewer 1913), *S. hermosa* new species, *S. lucifer* new species, *S. manauara* Pinto-da-Rocha 1994, *S. onorei* new species, *S. ortizi* Roewer 1952 and *S. singularis* (H. Soares 1970).

Distribution.—BRAZIL: Amazonas. COLOMBIA: Meta. ECUADOR: Napo; Pastaza and Tungurahua. PERU: Loreto and San Martín.

Santinezia angelica Roewer 1963
(Fig. 48)

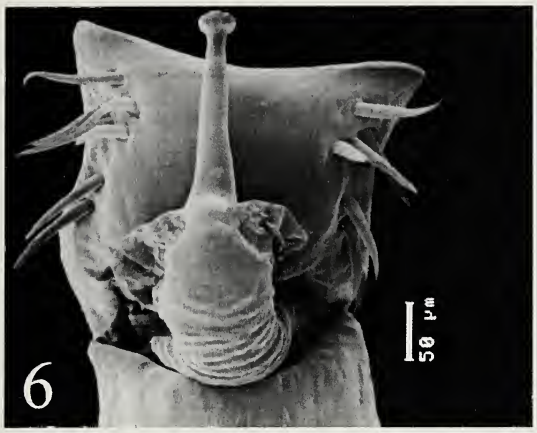
Santinezia angelica Roewer 1963: 69, figs. 43–44 (types SMF 12702, male holotype, 1 female paratype SMF 12723, male and female paratypes, not examined).

Type locality.—COLOMBIA: *Meta:* Parque Nacional Serranía de la Macarena (02°55′N, 73°50W), Zanza, 450–550 m.

Diagnosis.—Carapace behind eye mound, areas I–III and posterior margin of scute with white circles; free tergite I with a pair of spines; pedipalpal femur with mesal median spine; tibia IV of male with two basal ventral tubercles. Male tarsal counts: 8, 17–18, 8, 10. Compared to the species possessing white circles on scute; *S. gracilis*, *S. hermosa*, *S. singularis*, *S. ortizi*. Closest to *S. ortizi* by the white circles forming well defined transverse rows and by the black spines of area III. Distinguished from it by scutal grooves not delineated in black and by spines of eye mound separated at base.

Santinezia gigantea (Roewer 1913)
(Figs. 6, 7, 49)

Inezia gigantea Roewer 1913: 393, fig. 154–155 (type SMF two male syntypes, not examined).



Figures 6–7.—*Santinezia gigantea* (Roewer 1913) male from Nachiyacu (PUCQ), distal part of penis: 6. Dorsal view; 7. Same, lateral view. Scale bars = 0.05 mm.

Santinezia gigantea: Roewer 1923: 553; Roewer 1932: 290; Soares & Soares 1948: 618.

Type locality.—Roewer gave only "Santa Inez, Ecuador", but there are many places with this name in Ecuador. The accurate locality; ECUADOR: *Tungurahua:* Hacienda Santa Ines (1°25′S, 78°12′W; 1244 m), Brown (1941: 846) cited "An hacienda on the Baños-Canelos trail in the heart of the humid subtropical forest. It is on the north bank of the Rio Pastaza about half way from Rio Mapoto to Rio Topo. It is now rather run down. Faunistically it is about the same as Rio Mapoto (q May) . It was occupied for some time by Haensch and it is the type of locality for many species collected by him and at earlier times by Spruce, Buckley and Stübel."

Material examined.—ECUADOR: *Napo*: 1 ♂, Archidona: Cueva de Lagarto, 30 March 1991, P. Zambone (PUCQ); 1♂, Archidona: Nachiyacu, December 1986, R. Ramirez (MZUSP); 1♂, Nachiyacu, Pared de "El Cañon", December 1996, R. Ramirez (PUCQ); 1♂, Nachiyacu, "grieta en la roca", 5 December 1986, M. Gavilanes (MNRJ 5508); 1♂, El Cañon, 19 April 1991, R. Sandoya (PUCQ).

Diagnosis.—No white circles; free tergite I without a pair of spines; pedipalpal femur without mesal median spine; tibia IV of male with one ventro medial high tubercle. Male tarsal counts: 9, 14, 10, 11. Compared to *S. lucifer*, *S. manauara* and *S. onorei* by the absence of white circles and contrasting black spines. All these four species are very similar. *S. gigantea* and *S. lucifer* share the presence of a tooth on each lateral back corner of scute. *S. gigantea* has scute outline more normal, not so rounded posteriorly as in *S. lucifer*.

Supplementary description.—*Male genitalia* (Figs. 6, 7)*:* Ventral plate not cleft in distal border, distal corners projected in acute flange with two very small setae. With four groups of setae: two straight latero-basal, two slightly curved latero-distal, 1–2 dorso-lateral distal, one slightly curved lateral-apical. Stylus smooth, arising straight from glans. Apex bent in obtuse angle, not depressed nor swollen, with apical ridges, bearing well developed spiniform ventro-distal stylar apophysis.

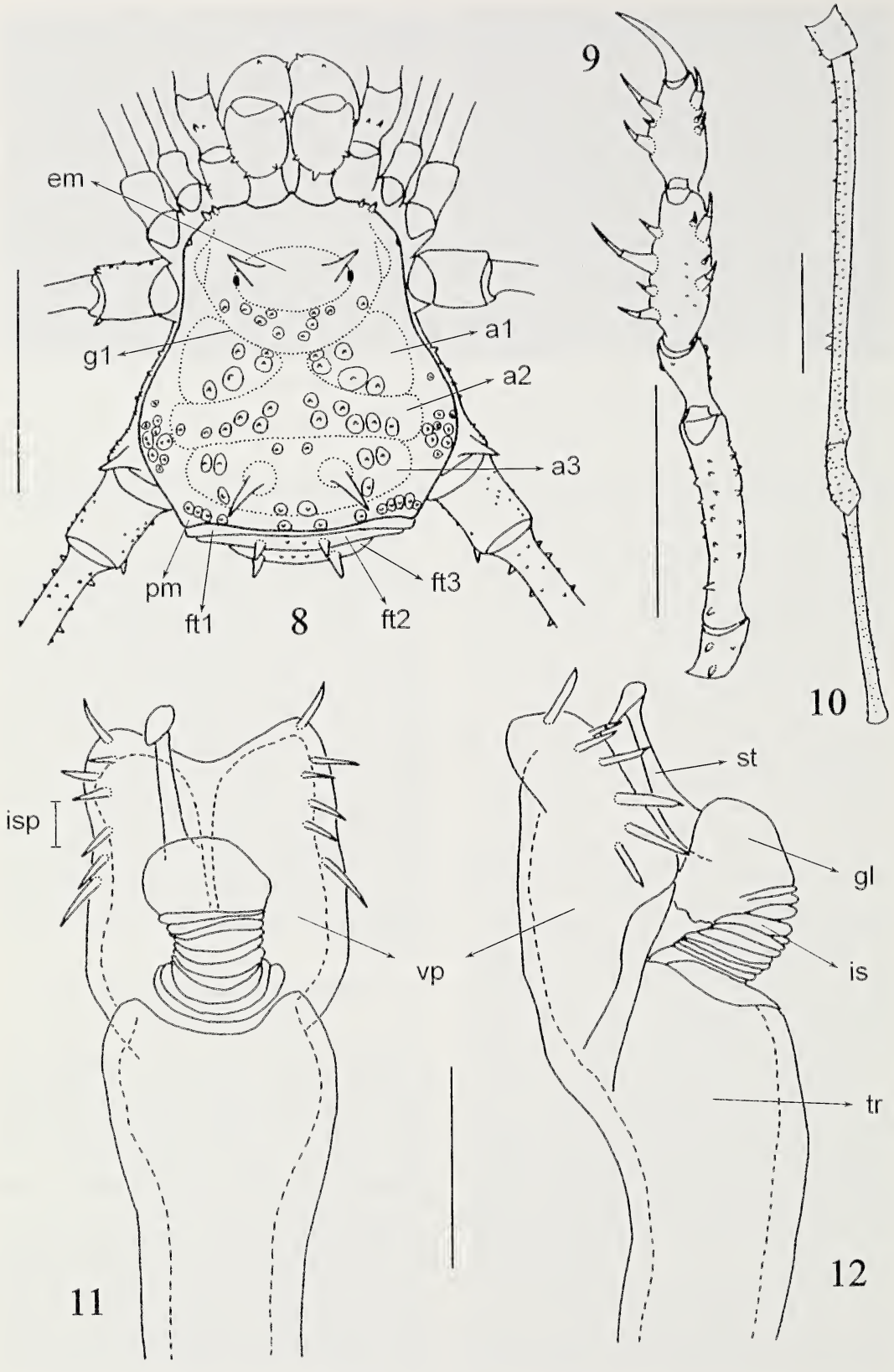
Distribution (Fig. 49).—ECUADOR: *Napo:* Archidona (0°55′S, 77°48′W): Cueva del Lagarto; Nachiyacu (0°50′S, 77°47′W). *Tungurahua:* Hacienda Santa Ines (1°25′S, 78°12′W).

Santinezia gracilis new species
(Figs. 8–12, 49)

Material examined.—*Male holotype:* ECUADOR: *Napo:* Papallacta, 19 September 1991, E.S. Ross (CAS). *Paratype:* ECUADOR: *Napo:* 1 ♀, Limoncocha, 240 m, February 1979, L. Burnham (MCZ).

Etymology.—From Latin for slender, referring to the lightly built habitus.

Diagnosis.—Carapace behind eye mound, areas I–III and lateral and posterior margins of scute with white circles; free tergite I without a pair of spines; pedipalpal femur without mesal median spine; tibia IV of male with one basal ventral tubercle. Male tarsal counts: 8,


em
g1
a1
a2
a3
pm
ft1
ft2
ft3
8
9
10
isp
vp
st
gl
is
tr
11
12

13–14, 9, 10; female 7, 11–12, 8, 9. Compared to the species possessing white circles on scute; *S. angelica*, *S. hermosa*, *S. singularis*, *S. ortizi*. Closest to *S. hermosa* and *S. singularis* by the absence of black areas and white circles not organized in rows. Distinguished from both by the presence of clusters of white circles in lateral areas.

Male holotype.—*Measurements (mm):* Dorsal scute length 7.0; width 6.6; cephalothorax length 3.1; width 4.8; pedipalpal femur 3.5; femur IV 16; leg I 22; II 48; III 35; IV 49. *Dorsal scutum* (Fig. 8): Anterior border with two paramedian tubercles and two smaller lateral ones. Eye mound with two sharp divergent high spines and one pair of posterior tubercles. Carapace with two tubercle pairs behind eye mound. Lateral margin of scutum with 8–11 tubercles concentrated between grooves II–III. Area I with 10 tubercles in each half; areas II–III with six tubercles; area III with two sharp divergent high spines. Posterior border with 13 tubercles. Free tergite I with pair of median tubercles; II–III with pair of spines; II with two tubercles between spines; III with three tubercles between spines. Anal operculum with one transverse median row of tubercles reaching posterior border. *Venter:* Coxa I with median row of tubercles (seven larger), three broader apical, five smaller posterior; coxa II with median row of six tubercles, three anterior, seven posterior, four apical; coxa III with median row of seven tubercles, eight posterior, seven apical; coxa IV with scattered tubercles, one pair of low apophyses near the stigmata. Stigmatic area and free sternites with one row of low setiferous tubercles. *Chelicera:* Basichelicerite with eight tubercles; hand with many frontal tubercles; fixed finger with four teeth; movable finger with three teeth. *Pedipalpus* (Fig. 8): Coxa with three ventral tubercles. Trochanter with three ventral tubercles. Femur with retrolateral row of nine tubercles, one dorsal row of eight (apical long and sharp), two ventral rows of tubercles (ectal with eight larger, mesal with six larger). Patella granular (especially dorsally). Tibia and tarsus dorsally granular, with four mesal (IiIi) and four ectal (IiIi) socketed spines. *Legs* (Fig. 10): Coxa I dorsally with one larger anterior tubercle, one smaller posterior; coxa II with one large tubercle next to opening of scent gland, one small posterior; coxa III with one anterior small tubercle; coxa IV with scattered latero-dorsal tubercles, one apical apophysis long and sharp, with tuberculate base. Trochanter I–IV granular; III–IV with one prolateral and retrolatero-apical larger tubercles. Femora III–IV with two dorso-apical sharp tubercles; IV with two dorsal rows of tubercles, one retrolateral row with five larger next to base and two in distal third, two ventral rows. Tibia IV with two ventral tubercles (basal larger). Tarsal articles: 8/ 13–14/9/10, distitarsi I and II with three articles. *Male genitalia* (Figs. 11, 12): Ventral plate with shallow cleft in distal border, distal corners with flange restricted to two small triangular apical lobes. With four groups of setae: three straight latero-basal, two short straight latero-distal, 0–1 short straight dorso-lateral distal, one straight latero-apical. Stylus smooth, arising straight from glans. Apex bent in obtuse angle, not depressed nor swollen, with apical ridges, bearing short spiniform ventro-distal stylar apophysis. *Color:* Body background and legs dark brown to black. Pedipalpal tibia-tarsus, eye mound and middle of anterior border with black reticule. Tubercles of carapace, lateral border, posterior border and areas I–III circled in white. Spines of eye mound and free tergites yellowish. Metatarsi and tarsi I–IV yellowish.

Female paratype (MCZ).—Anterior margin of carapace with two median small tubercles and two lateral larger on each side. Eye mound with three white-encircled setifer-

←

Figures 8–12.—*Santinezia gracilis* new species, male holotype from Papallacta (CAS): 8. Habitus, dorsal view; 9. Left pedipalpus, ventral view; 10. Right leg IV trochanter to tibia, dorsal view; 11. Distal part of penis, dorsal view; 12. Same, lateral view. Scale bars = 5 mm (Figures 8–10), 0.05 mm (Figures 11–12). Habitus (Fig. 8): a1, a2, a3 = areas I, II and III; em = eye mound; ft 1, ft2, ft3 = free tergites I, II and III; g1, g2, g3 = groove I, II and III; pm = posterior margin. Penis (Fig. 11–12): gl = glans; is = inflatable sac of glans; isp = insertal portion of ventral plate; st = stylus; tr = truncus; vp = ventral plate.

ous tubercles around the eyes. Carapace with four + four white-encircled setiferous tubercles behind eye mound. Area I with five + four white-encircled setiferous tubercles, area II with five + five white-encircled setiferous tubercles in the middle two-thirds; area III with two sharp divergent high spines, two + two white-encircled setiferous tubercles external to them, two + two in the ill-defined area IV. Free tergite I with two paramedian granules, II–III with two paramedian spines and three setiferous tubercles between them; free tergite III with one tubercle lateral to spines. Chelicera and pedipalpus as in male. Tarsal articles: 7/11–12/8/9. Distitarsi I–II with three articles. Color as in male.

Distribution (Fig. 49).—ECUADOR: *Napo:* Limoncocha, 240 m (00°23′S, 76°37′W); Papallacta (00°22′S, 78°08′W).

Santinezia hermosa new species
(Figs. 13–18, 48)

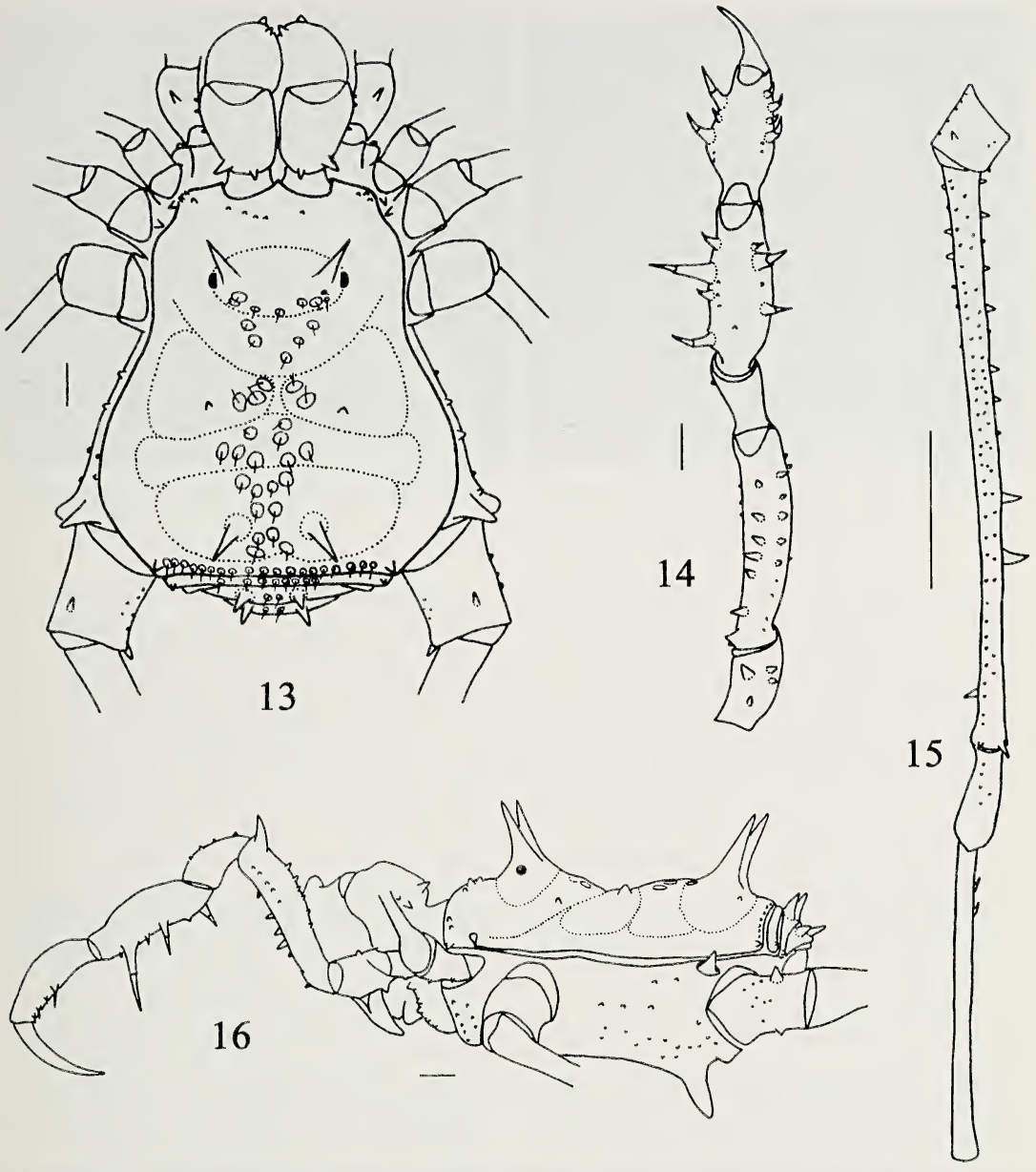
Type locality.—PERU: *Loreto:* Alto Rio Samiria.

Material examined.—*Holotype male:* PERU: *Loreto:* Upper Río Samiria, May 1990, T. Erxlin & D. Silva, Iquitos (MUSM). *Paratypes:* ECUADOR: *Napo:* 1 ♂, 1♀, 25 km E. of Puerto Napo, Selva Aliñahuí, 450 m, January–February 1991, E. S. Ross (CAS); 1 female, same data (MNRJ 5612); 1♂, 3 ♀, same locality, February 1999, E. Ross (MNRJ 5780); 1♂, 1♀, 20 km E. of Puerto Napo, Aliñahuy, February 1994, E. Ross (MNRJ 5729); 1♂, 4♀, same data (CAS);1 ♀, 1 immature, Papallacta, 19 September 1991, E.S. Ross (CAS). PERU: *Loreto:* 1♀, Iquitos, April 1931, R.C. Shannon (USNM); 1 male, Jenaro Herrera, 100 m, 23 August 1988, D. Silva (MZSP); 1♂, 2♀, Parque Nacional Pacaya-Samiria, *Pithecia,* 100 m, August 1989, D. Silva (MUSM).

Etymology.—From the Spanish "hermosa" for beautiful, referring to the nice combination of colors of the body.

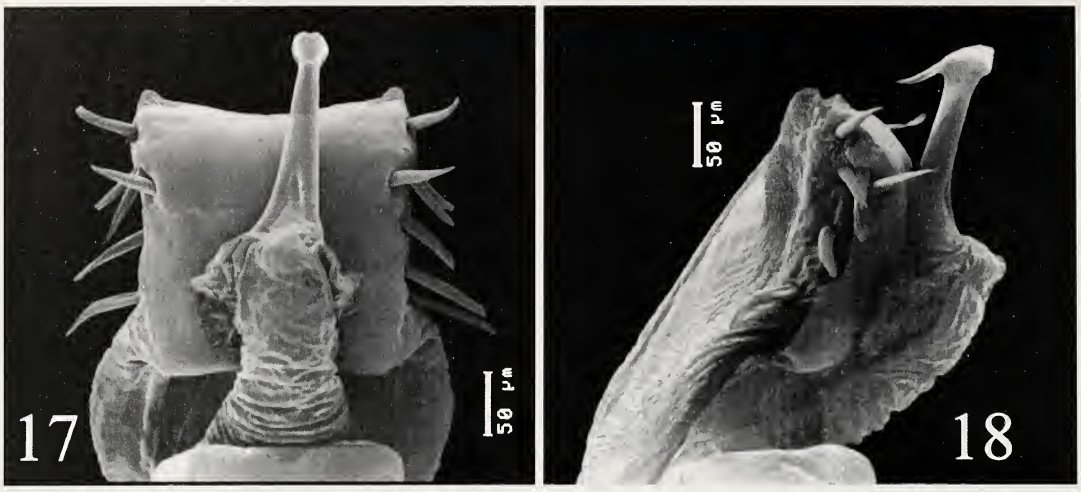
Diagnosis.—Eye mound and carapace behind it, areas I–III and posterior margin of scute with white circles restricted to the middle; free tergites I–III with a transverse row of white circles; free tergite I without a pair of spines; pedipalpal femur without mesal median spine; tibia IV of male with two long basal ventral tubercles. Male tarsal counts: 8, 14, 8, 9. Compared to the species possessing white circles on scute; *S. angelica*, *S. gracilis*, *S. singularis*, *S. ortizi*. Closest to *S. gracilis* and *S. singularis* by the absence of black areas and white circles not organized in rows. Distinguished from both by the white circles restricted to mid-fourth of scutal areas.

Male holotype.—*Measurements (mm):* Dorsal scute length 8.4; width 7.3; cephalothorax length 4.0; width 5.3; pedipalpal femur 4.3; femur IV 18.5; leg I 25; II 52; III 37; IV 54. *Dorsal scutum* (Fig. 13): Anterior border with eight paramedian tubercles. Eye mound with two sharp divergent high spines, eight posterior setiferous tubercles. Carapace with five tubercle pairs behind eye mound. Lateral margin of scutum smooth. Area I with one high tubercle in each half, five setiferous tubercles between them; area II with eight setiferous tubercles in the middle; area III with two sharp divergent high spines and 10 tubercles between them. Posterior border with 20 setiferous tubercles. Free tergite I with six median and two lateral tubercles; II–III with pair of spines and two setiferous tubercles between them. Anal operculum with small tubercles. *Venter:* Coxa I with row of 5–6 median large tubercles, 4 apical, 2–3 anterior, 4–6 posterior; coxa II with median row of 5–7 tubercles, 5 posterior, 4 apical; coxa III with median row of 7 tubercles, 7–8 posterior, 5 apical; coxa IV with an irregularly disposed tubercles, one pair of apophyses; area between apophyses and anal operculum strongly depressed. Stigmatic area and free sternites with one row of small tubercles. *Chelicera:* Basichelicerite with 5 tubercles; hand with one longitudinal frontal row of tubercles (distal one stouter); fixed finger with 5 broad low teeth; movable finger with 4 teeth. *Pedipalpus* (Fig. 14): Coxa with two ventral tubercles. Trochanter with four ventral tubercles (two higher), one dorsal. Femur with retrolateral row of 9–10 tubercles, 2 ventrodistal, 1 retrolateral subdistal, 1 dorsal row of 9 (apical long and sharp), one ventral row of six larger tubercles. Patella granular (especially dorsally). Tibia with coarse dorsal tuberculation, with four mesal (IiIi), three ectal (Iii) socketed spines. Tarsus with 3 mesal (IiI) and 4 ectal (Iiii) socketed spines, with small dorsal tubercles. *Legs* (Fig. 15): Coxa I dorsally with one larger anterior tubercle, one smaller posterior; coxa II with one high tubercle next to opening of scent gland, one small posterior fused with an other of III; coxa



Figures 13–16.—*Santinezia hermosa* new species, male holotype from Río Samiria (MUSM): 13. Habitus, dorsal view; 14. Left pedipalpus, ventral view; 15. Right leg IV trochanter to tibia, dorsal view; 16. Habitus, lateral view. Scale bars = 5 mm.

III with one anterior small tubercle fused with other of IV; coxa IV with scattered tubercles, one apical long and sharp apophysis. Trochanter I with 3 ventral tubercles (central broad and high) II with 3 ventral, 2 retrolateral; III with 3 prolateral, 3 retrolateral, 5ventral; IV with one dorsal larger tubercle and some smaller. Femora I–IV with small sharp pointed tubercles; III–IV with 2 dorso-apical sharp tubercles (retro larger); IV with one row of retrolateral tubercles, 1–2 long in the middle, one ventro-subapical long. Patellae III–IV with small tubercles. Tibia IV with retrolateral row of tubercles, anterior larger. Tarsal articles: 8/14/8/9, distitarsi I–II with 3 articles. *Male genitalia* (Figs. 17, 18): Ventral plate not cleft in distal border, distal corners with flange restricted to two small triangular apical lobes.



Figures 17–18.—*Santinezia hermosa* new species, male paratype from Parque Nacional Pacaya-Samiria (MUSM): 17. Distal part of penis, dorsal view; 18. Same, lateral view. Scale bars = 0.05 mm.

With four groups of setae: 2–3 straight latero-basal, two latero-distal, one dorso-lateral distal, one latero-apical. Stylus smooth, arising straight from glans. Apex bent in obtuse angle, distally truncated, not depressed nor swollen, with apical ridges, bearing well developed spiniform ventro-distal stylar slightly curved apophysis. *Color:* Body background dark brown, middle of carapace down to posterior border lighter. Pedipalpi, chelicerae, eye mound and middle of anterior margin of carapace light brown with black reticule. Spines of eye mound and free tergites contrasting yellowish neon green. Setiferous tubercles of dorsal scutum and free tergite I circled by broad white spots. Legs brown mottled with black.

Female paratype (MUSM 039).—*Measurements (mm):* Dorsal scute length 7.4; width 7.5; cephalothorax length 3.4; width 4.6; pedipalpal femur 3.9; femur IV 14.5; leg I 21; II 48; III 39; IV 47. Anterior margin with 1–2 median tubercles. Eye mound with 13 posterior setiferous tubercles. Carapace with 6 setiferous tubercles behind eye mound. Area I with one high tubercle on each half, five setiferous tubercles between them; area II with eight setiferous tubercles in the middle; area III with two sharp divergent high spines, 10 setiferous tubercles between them. Free tergites II–III with two spines and three setiferous tubercles between them; free tergite III with two tubercles lateral to spines. *Chelicera:* basichelicerite with three tubercles; hand with one longitudinal frontal row of subequal tubercles; fixed finger with 4 teeth broad low and movable finger with 3. *Pedipalpus:* tibia and tarsus with 4 mesal (IiIi) and 4 ectal (IiIi) socketed spines. Leg IV with tubercles smaller than in male; ventral apophysis of coxa IV absent; trochanter IV with dorsal tubercle larger than in male. *Tarsal articles:* 8/13–14/8/9–10, distitarsi I–II with 3 articles. Posterior margin and free tergites yellowish.

Distribution (Fig. 48).—ECUADOR: *Napo:* 25 km E of Puerto Napo, Selva Aliñahuí, 450 m (01°03′S, 77°34′W). Papallacta (0°22′S, 78°08′W). PERU: *Loreto:* Alto Rio Samiria (05°12′S, 75°20′W); Iquitos (03°46′S, 73°15′W); Jenaro Herrera, 100 m (4°55′S, 73°45′W); Parque Nacional Pacaya-Samiria, *Pithecia,* 100 m (05°06′S, 74°50′W).

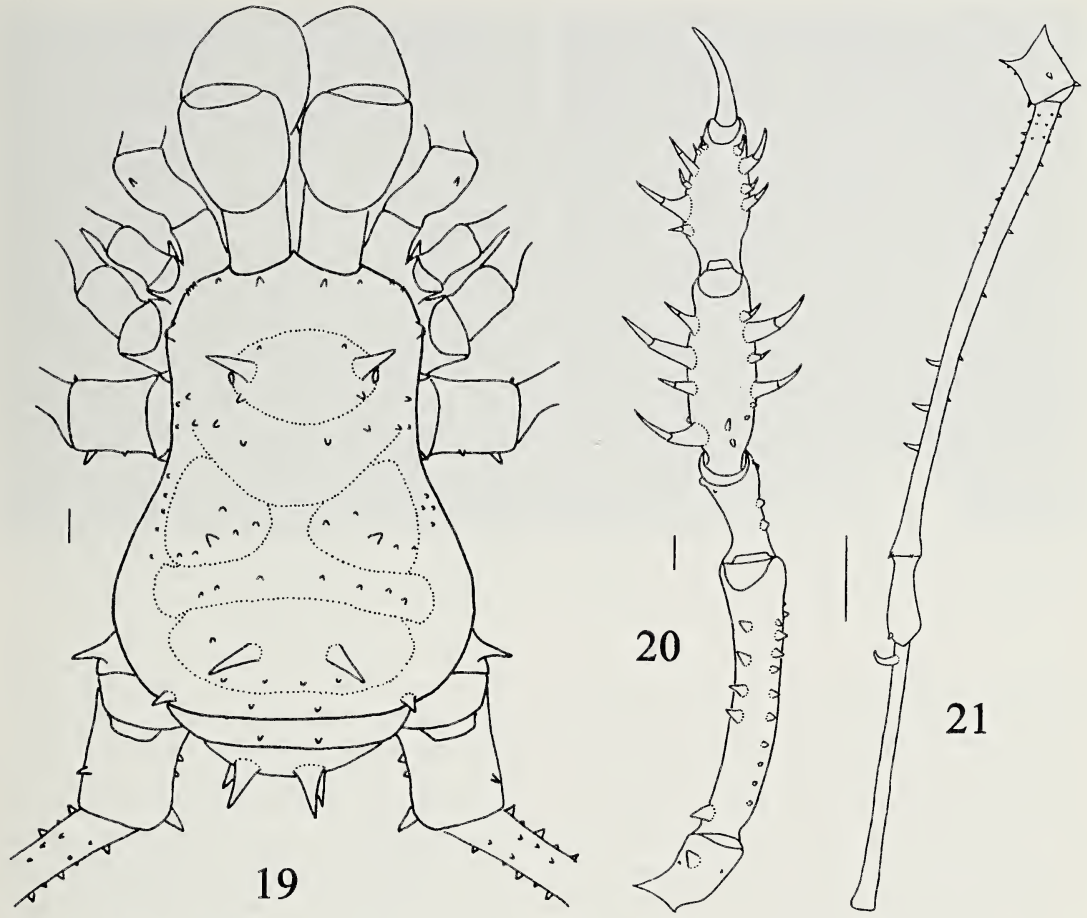
Remarks.—The paratype from Iquitos has more uniform overall color, and the round spots are more clearly marked.

Santinezia lucifer new species
(Figs. 19–23, 49)

Type locality (Fig. 49).—ECUADOR: *Pastaza:* Puyo (1°30′S, 77°59′W). Cueva del Alacran.

Material examined.—Male holotype: ECUADOR: *Pastaza:* Puyo: Cueva del Alacran, July 1986, G. Onore (PUCQ). Paratypes: 1♂, 2♀, same data (PUCQ).

Etymology.—The species name comes from the King of Darkness (although the name

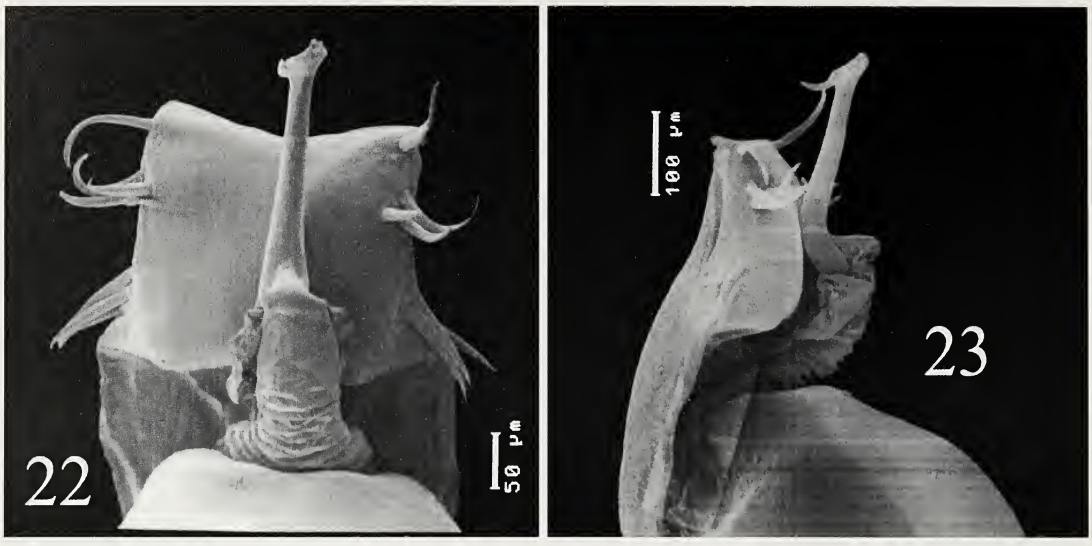


Figures 19–21.—*Santinezia lucifer* new species, male holotype from Cueva del Alacran (PUCQ): 19. Habitus, dorsal view; 20. Left pedipalpus, ventral view; 21. Right leg IV trochanter to tibia, dorsal view. Scale bars = 5 mm.

means "Bringer of Light"), referring to the cave habitat.

Diagnosis.—No white circles; free tergite I without a pair of spines; pedipalpal femur without mesal median spine; tibia IV of male with one long curved basal ventral tubercle. Male tarsal counts: 10, 17, 10, 11. Compared to *S. gigantea*, *S. manauara* and *S. onorei* by the absence of white circles and contrasting black spines. All these four species are very similar. *S. gigantea* and *S. lucifer* share the presence of a tooth on each lateral back corner of scute. *S. lucifer* has body outline more strongly pyriform than *S. gigantea*.

Male holotype.—*Measurements (mm):* Dorsal scute length 13.1; width 10.1; cephalothorax length 7.0; width 7.6; pedipalpal femur 7.2; femur IV 31; leg I 51; II 97; III 73; IV 91. *Dorsal scutum* (Fig. 19): Anterior border with two sharp paramedian tubercles and three smaller lateral. Eye mound with two sharp divergent high spines, pair of anterior and posterior tubercles. Carapace with four tubercle pairs beside and behind eye mound. Lateral margin of scutum with 6–7 tubercles between grooves I–II. Area I with 5–6 tubercles in each half (one pair stouter); area II with transverse row of 7 tubercles; area III with 5 tubercles and 2 sharp divergent high spines. Posterior border with pair of high lateral tubercles and two paramedian. Free tergite I with pair of tubercles; II–III with pair of spines. *Venter:* Coxa I with row of median tubercles, 3 apical, 4 anterior, 1 posterior; coxa II with median row of 7 tubercles, 4 anterior, 4 posterior, 5 apical; coxa III with median row of 6 tubercles, 5 posterior in row, 5 apical; coxa IV with a few scattered tubercles,



Figures 22–23.—*Santinezia lucifer* new species, male paratype from Cueva del Alacran (PUCQ): 22. Distal part of penis, dorsal view; 23. Same, lateral view. Scale bars = 0.05 mm.

one pair of stout apophyses near the stigmata. *Chelicera:* Basichelicerite with 5 tubercles; hand with 16–18 frontal tubercles; fixed finger with 4 teeth; movable finger with 4 teeth. *Pedipalpus* (Fig. 20): Coxa with two ventral tubercles. Trochanter with one high ventral tubercle, two dorsal. Femur with retrolateral row of 9–11 tubercles, 2 prolateral, 1 dorsal row of 6 (apical long and sharp), one ventral row of 5–6 tubercles. Patella granular. Tibia dorsally granular, with 4–5 mesal (IiIi (IiiIi), 4 ectal (IiIi) socketed spines. Tarsus with 5 mesal (iIiIi), 4 ectal (IiIi) socketed spines, dorsally smooth. *Legs* (Fig. 21): Coxa I dorsally with one larger anterior tubercle, one smaller posterior; coxa II with one tubercle anterior to opening of scent gland, one small posterior; coxa III with one anterior small tubercle; coxa IV with 10–12 latero-dorsal, one apical long and sharp, Trochanter I–IV granular; III–IV with larger retrolatero-apical tubercles; IV with 1 prolateral, 2 ventral and 1 dorsal larger. Femora I–IV granular; III–IV with two dorso-apical sharp tubercles; IV with 1–3 long curved tubercles in retrolateral distal half. Tibia IV with curved basal retrolateral tubercle. Tarsal articles: 10/17/10/11, distitarsi I–II with three articles. *Male genitalia* (Figs. 22, 23): Ventral plate not cleft in distal border, distal corners without flange. With four groups of setae: 3 straight latero-basal, 2 curved latero-distal, 1 dorso-lateral distal, 1 latero-apical long and sinuous, with distal third depressed. Stylus smooth, arising straight from glans. Apex bent in obtuse angle, heavily depressed, not swollen, with apical high papillae, bearing well developed spiniform ventro-distal curved stylar apophysis. *Color:* Body background greenish light brown, legs and pedipalpus dark brown. Chelicerae and eye mound with black reticule. Tubercles of dorsal scutum white. Spines of eye mound, area III and free tergites yellowish. Area III and base of spines blackened.

Female paratype.—*Measurements (mm):* Dorsal scute length 10.8; width 9.7; cephalothorax length 4.9; width 6.8; pedipalpal femur 6.1; femur IV 26; leg I 41; II 87; III 63; IV?. Eye mound with two anterior tubercles. Carapace with seven tubercles. Lateral border with nine tubercles. Area I with 4–5 tubercles; area II with 7–10; area III with 3. Posterior border with 4–6 tubercles (the lateral larger). Without larger tubercles in femur and tibia IV. *Pedipalpus:* tibia and tarsus with 4 mesal (IiIi) and 4 ectal (IiIi) socketed spines.

Santinezia manauara Pinto-da-Rocha 1994
(Fig. 48)

Santinezia manauara Pinto-da-Rocha 1994: 29, figs. 1–2 (type INPA, male holotype; MZSP; MCN, paratypes, examined).

Type locality (Fig. 48).—BRAZIL: *Amazonas:* Manaus (03°08′S, 60°01′W).

Diagnosis.—No white circles; free tergite I without a pair of spines; pedipalpal femur with mesal median spine; tibia IV of male with one medio ventral tubercle. Tarsal counts: 10, 18, 11, 12. Compared to *S. gigantea*, *S. lucifer* and *S. onorei* by the absence of white circles and contrasting black spines. All these four species are very similar. *S. manauara* can be distinguished from the other three by the presence of a mesal subapical spine on pedipalpal femur.

Santinezia onorei new species
(Figs. 24–28, 49)

Type locality (Fig. 49).—ECUADOR: *Pastaza:* Taracoa (1°25′S, 76°47′W).

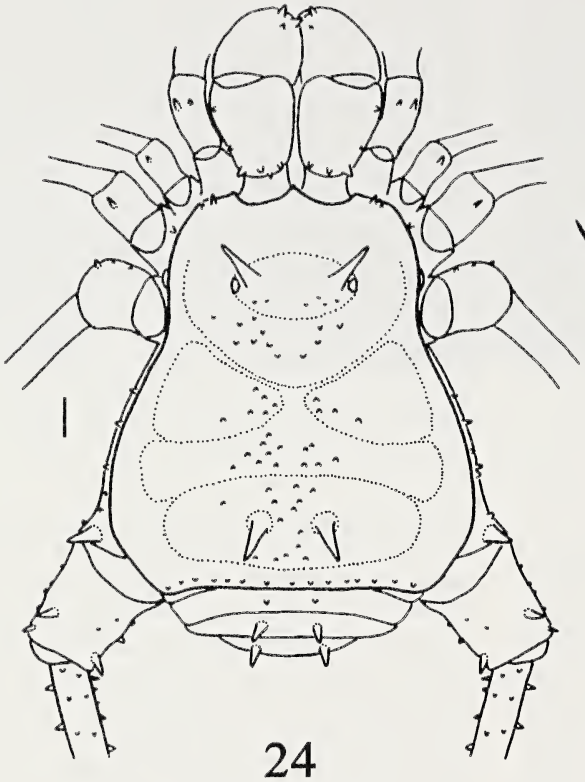
Material examined.—Male holotype: ECUADOR: *Pastaza:* Taracoa, 27 November 1983, M. Garcia (PUCQ).

Etymology.—Species name is in honor of Giovanni Onore (PUCQ), who gave a great impetus on the study of arthropods of Ecuador.

Diagnosis.—No white circles; free tergite I without a pair of spines; pedipalpal femur without mesal median spine; tibia IV of male with one long basal ventral tubercle. Tarsal counts: 7–8, 13–14, 9, 10. Compared to *S. gigantea*, *S. lucifer* and *S. manauara* by the absence of white circles and contrasting black spines. All these four species are very similar. *S. onorei* can be distinguished from the other three by the granules of scutal areas restricted to the mid portion.

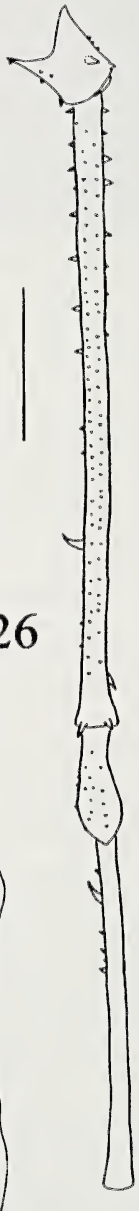
Male holotype.—*Measurements (mm):* Dorsal scute length 9.4; width 8.6; cephalothorax length 4.8; width 6.0; pedipalpal femur 5.1; femur IV 21; leg I 31; II 65; III 48; IV 67. *Dorsal scutum* (Fig. 24): Anterior border with two paramedian tubercles and two lateral on each side. Eye mound with two sharp divergent high spines, 5 pairs of posterior tubercles. Carapace with 11 tubercles behind eye mound. Lateral margin of scutum smooth. Area I with 6 tubercles in each half (one pair stouter); area II with 15 tubercles; area III with two sharp divergent high spines and 14 tubercles between and behind the spines. Posterior border with 20 tubercles. Free tergite I with two median tubercles; II–III with pair of spines. *Venter:* Coxa I with row of 4 median larger tubercles, 4 apical larger, 4 anterior, 5 posterior; coxa II with median row of 6 tubercles, 5 posterior, 4 apical (two geminated); coxa III with median row of 8 tubercles, 4 anterior, 6 apical; coxa IV with a few scattered tubercles, one pair of apophyses near the stigmata. Stigmatic area and free sternites with a median row of tubercles. *Chelicera:* Basichelicerite with eight tubercles; hand with one longitudinal row of frontal tubercles; fixed finger and movable finger with three teeth wide and low. *Pedipalpus* (Fig. 25): Coxa with two ventral tubercles. Trochanter with four ventral (two larger) tubercles. Femur with retrolateral row of eight-nine tubercles, three prolateral, one dorsal row of seven (apical long and sharp), one ventral row of six larger tubercles. Patella granular, especially dorsally. Tibia dorsally granular, with four mesal (IiIi), four ectal (IiIi) socketed spines. Tarsus with ectal and ventral rows of small socketed spines, dorsally smooth. *Legs* (Fig. 26): Coxa I dorsally with one larger anterior tubercle, one smaller posterior; coxa II with one tubercle next to opening of scent gland, one small posterior tubercle fused with one of coxa III; coxa III with one posterior tubercle fused with one of coxa IV; coxa IV with lateral row of four tubercles, one apical apophysis long and sharp. Trochanters I–II and IV with one dorsal and one ventral large tubercle; II–IV with one apical retrolateral larger than the others. Femora III–IV with one retrolateral basal larger tubercle, four high dorso-apical; IV with one high ventral tubercle, one retrolateral row, one tubercle in distal third much higher and curved. Patellae III–IV with small tubercles. Tibia IV with one ventral row of tubercles in proximal half, two larger proximal. Tarsal articles: 8/16/8/9, distitarsi I–II with 3 articles. *Male genitalia* (Figs. 27, 28): Ventral plate with shallow cleft in distal border, distal corners without flange. With four groups of setae: 3 straight latero-basal, 2 short straight latero-distal, 1 curved dorso-lateral distal, 1 curved latero-apical. Stylus smooth, arising straight from glans. Apex bent in obtuse angle, not depressed nor swollen, with apical ridges, bearing short spiniform ventro-distal stylar apophysis. *Color:* Body background brown carapace and area III darker. Pedipalpi, chelicerae, eye mound and median portion of anterior border with black reticule. Spines of eye mound and free tergites yellowish.

Female.—Unknown.

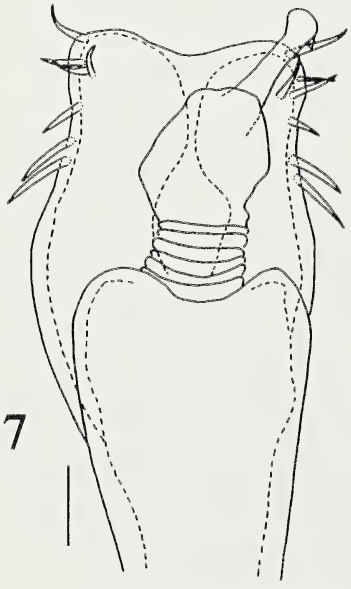


24

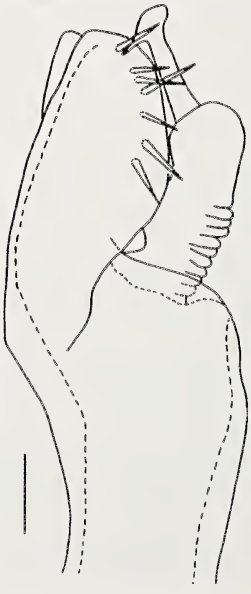
25



26



27



28

Santinezia ortizi Roewer 1952
(Fig. 48)

Santinezia ortizi Roewer 1952: 56, fig. 15, 15a–c (type SMF RII 9806/85, male holotype, not examined).

Type locality (Fig. 48).—PERU: *San Martín:* Puerto Huicte, near Uchiza, Rio Huallaga, above 600 m (8°27′S, 76°21′W).

Diagnosis.—*Santinezia* with femur IV of male straight, armed with one subapical ectal spur, one subbasal mesal and ectal spurs; trochanter IV of male with one apical ectal and mesal spurs; spines of area III and coxa IV black sharp contrasting with background; granules of areas I–III, posterior margin and free tergites circled by white rings. Basitarsus I of male swollen. Tarsal counts 7–8, 13–14, 9, 10. Genitalia undescribed. Compared to the species possessing white circles on scute; *S. gracilis*, *S. hermosa*, *S. singularis*, *S. angelica*. Closest to *S. angelica* by the white circles forming well defined transverse rows and by the black spines of area III. Distinguished from it by some scutal grooves sharply delineated in black and by spines of eye mound close together at base and diverging apically.

Distribution.—Known only from the type locality.

Santinezia singularis (H. Soares 1970), new combination
(Figs. 29–34, 48)

Carvalholeptes singularis H. Soares 1970b: 330, figs. 12–16 (type MNRJ 5080, male holotype and female paratype examined).

Type locality.—BRAZIL: *Amazonas:* Benjamin Constant.

Material examined.—Male holotype: BRAZIL: *Amazonas:* Benjamin Constant, May 1950, J.C.M. Carvalho & A. Viegas (MNRJ 5080). Paratypes: 1 female, same data (MNRJ 5080); 1 female, same data (MNRJ 5611).

Other material.—COLOMBIA: *Putumayo:* Santa Rosa (Kofan indian village), headwaters of Rio San Miguel, 2–25 October 1970, B. Malkin & P. Burchard (FMNH AK 10); 1♂, no further data, N. Leist (SMNK). PERU: *Loreto:* 1♂, Jenaro Herrera, 28 August 1988, V. & B. Roth (CAS).

Diagnosis.—White circles on eye mound, between eye mound and groove I, on areas I–III, on posterior margin and on free tergite I. Free tergite without spines. Male femur IV without prolateral subapical tubercle. Tibia IV with two ventrobasal tubercles. Tarsal segmentation on male: 8, 14, 9, 9; female 8, 12–13, 9, 10. Compared to the species possessing white circles on scute; *S. angelica*, *S. gracilis*, *S. hermosa*, *S. ortizi*. Closest to *S. gracilis* and *S. hermosa* by the absence of black areas and white circles not organized in rows. Distinguished from *S. hermosa* by the white circles occupying of scutal areas and from *S. gracilis* by the absence of clusters of white circles in lateral areas.

Description (SMNK).—*Male genitalia* (Figs. 33, 34)*:* Ventral plate with shallow cleft in distal border, distal corners with flange restricted to two small triangular apical lobes. With four groups of setae: 3 straight latero-basal, 2 short straight latero-distal, 1 short straight dorso-lateral distal, 1 short curved latero-apical. Stylus smooth, arising straight from glans. Apex bent in obtuse angle, not depressed nor swollen, with apical ridges, bearing short curved spiniform ventro-distal stylar apophysis.

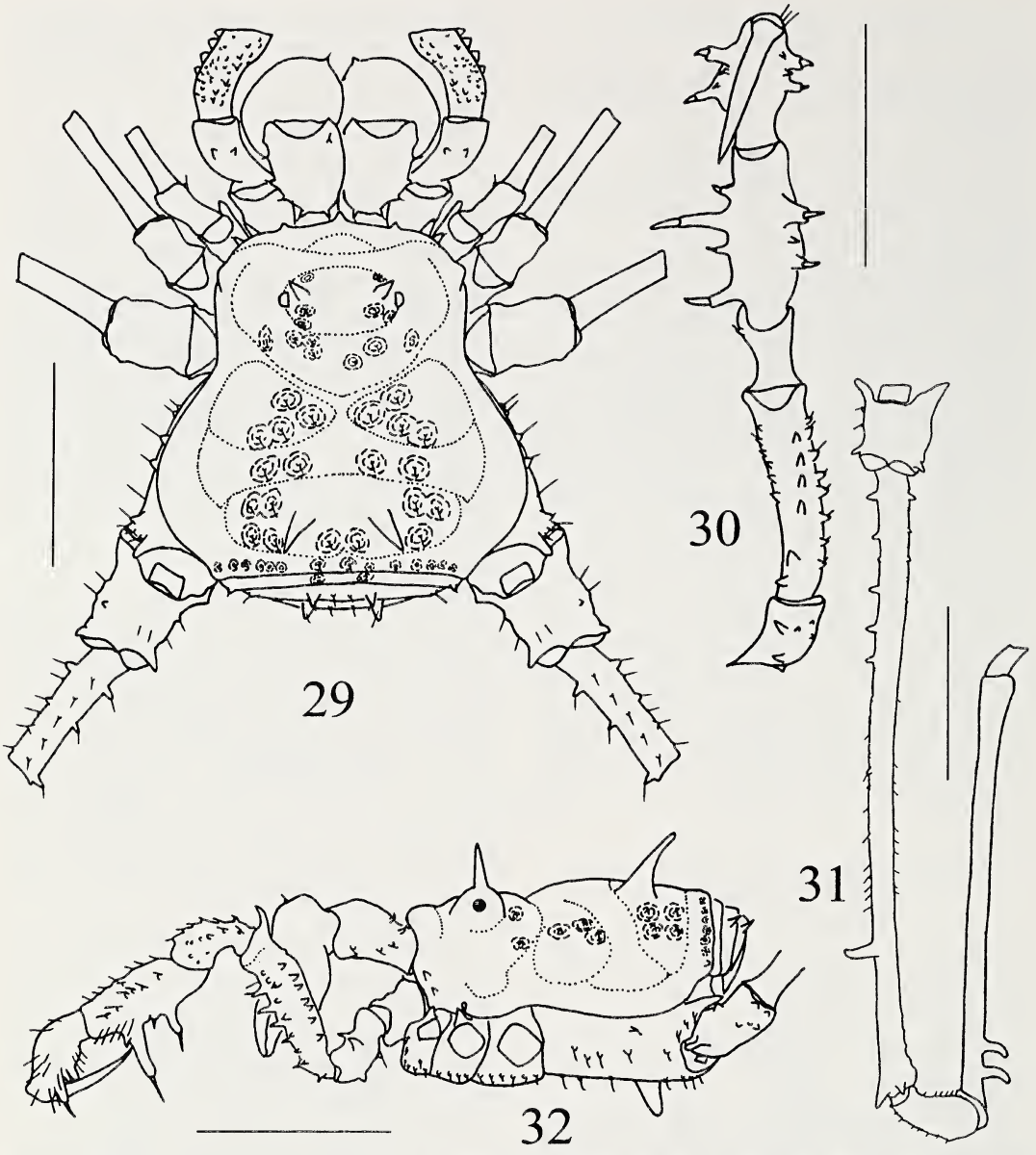
Distribution (Fig. 48).—BRAZIL: *Amazonas:* Benjamin Constant (04°22′59″S, 70°01′52″W). COLOMBIA: *Putumayo:* Santa Rosa de Guamez (Kofan Indian village), headwaters of Rio San Miguel (0°48′N, 75°27′W). PERU: *Loreto:* Jenaro Herrera (04°55′S, 73°45′W).

Santinezia festae species group

Diagnosis.—Paramedian spines of scutal area III very high (character 1, state 0) [P]. Paramedian spines of scutal area I high and sharp (character 2, state 1) [A]. Basal group of setae of ventral plate three, rarely two,

←

Figures 24–28.—*Santinezia onorei* new species, male holotype from Taracoa (PUCQ): 24. Habitus, dorsal view; 25. Left pedipalpus, ventral view; 26. Right leg IV trochanter to tibia, dorsal view; 27. Distal part of penis, dorsal view; 28. Same, lateral view. Scale bars = 5 mm (Figs. 24–26), 0.05 mm (Figs. 27–28).



Figures 29–32.—*Santinezia singularis* (H. Soares 1970), male holotype from Benjamin Constant (MNRJ 5080): 29. Habitus, dorsal view; 30. Left pedipalpus, ventral view; 31. Right leg IV trochanter to tibia, dorsal view; 32. Habitus, lateral view. Scale bars = 5 mm.

forming nearly longitudinal row (character 11, state 0) [P]. General shape of ventral plate roughly rectangular (character 13, state 0) [P]. Ventral apophysis of coxa IV located far from stigmata, in the middle of coxa (character 19, state 1) [A]. Tibia IV of male without mesal row of spines occupying proximal half (character 21, state 0) [P]. Tibia IV of male without two-three ventro-mesal short spines in basal fourth, the most proximal hook-shaped curved (character 23, state 1) [P]. Femur IV of male without accessory spines ecto-apical (character 25, state 0) [P]. Femur IV of male with two apophyses accessory to stout curved sub apical ectal apophysis (character 27, state 2) [A]. Femur IV of male with two or three short submedial mesal apophyses (character 28, state 1) [A]. Femur IV of male ectal and mesal with row of subequal spines (character 30, state 1) [A]. Pedipalpal femur of male cylin-

Figures 33–34.—*Santinezia singularis* (H. Soares 1970), male from Amazonas (SMNK): 33. Distal part of penis, dorsal view; 34. Same, lateral view. Scale bars = 0.05 mm.

drical (character 32, state 1) [A]. Easily distinguished from the other groups in *Santinezia* by the advanced position of the paired ventral apophyses of coxa IV.

Included species.—*Santinezia arthrocentrica* (Mello-Leitão 1943) and *S. festae* (Roewer 1925).

Santinezia arthrocentrica (Mello-Leitão 1943), new combination
(Figs. 35–40, 48)

Macuchicola arthrocentrica Mello-Leitão 1943: 4, figs. 1–2; Soares & Soares 1948: 606 (type MNRJ 5004, male holotype).

Type locality.—ECUADOR: *Pichincha:* Macachi (misspelled in the original description as "Macuchi"), 2940 m (00°31′S, 78°34′W).

Material examined.—Male holotype: ECUADOR: *Pichincha:* Macachi, D. Frizzell (MNRJ 5004).

Diagnosis.—Anterior margin of carapace with four tubercles, region behind eye mound with several scattered tubercles. Area II covered by scattered tubercles. Coxa IV with two larger tubercles pointed laterally. Trochanter IV with one large dorsal tubercle. Dorsal scute with yellowish cross. Distinguished from *S. festae* by bicolor pattern of scute and the pointed tubercles of coxa IV of male.

Description.—*Male holotype genitalia* (Figs. 39, 40): Ventral plate with distal border entire, distal corners without flange. With two groups of setae: 3 straight latero-basal, 3 latero-distal. Stylus with distal ring of small spines, arising straight from glans. Apex bent in obtuse angle, not depressed nor swollen, with apical ridges, without stylar apophysis.

Distribution (Fig. 48).—Known only from the type locality.

Remarks.—*Macuchicola arthrocentrica* possesses all the features of the genus *Santinezia* and the monotypic genus *Macuchicola* has no support (see "Remarks" item on *Santinezia*).

Santinezia festae (Roewer 1925), new combination
(Fig. 48)

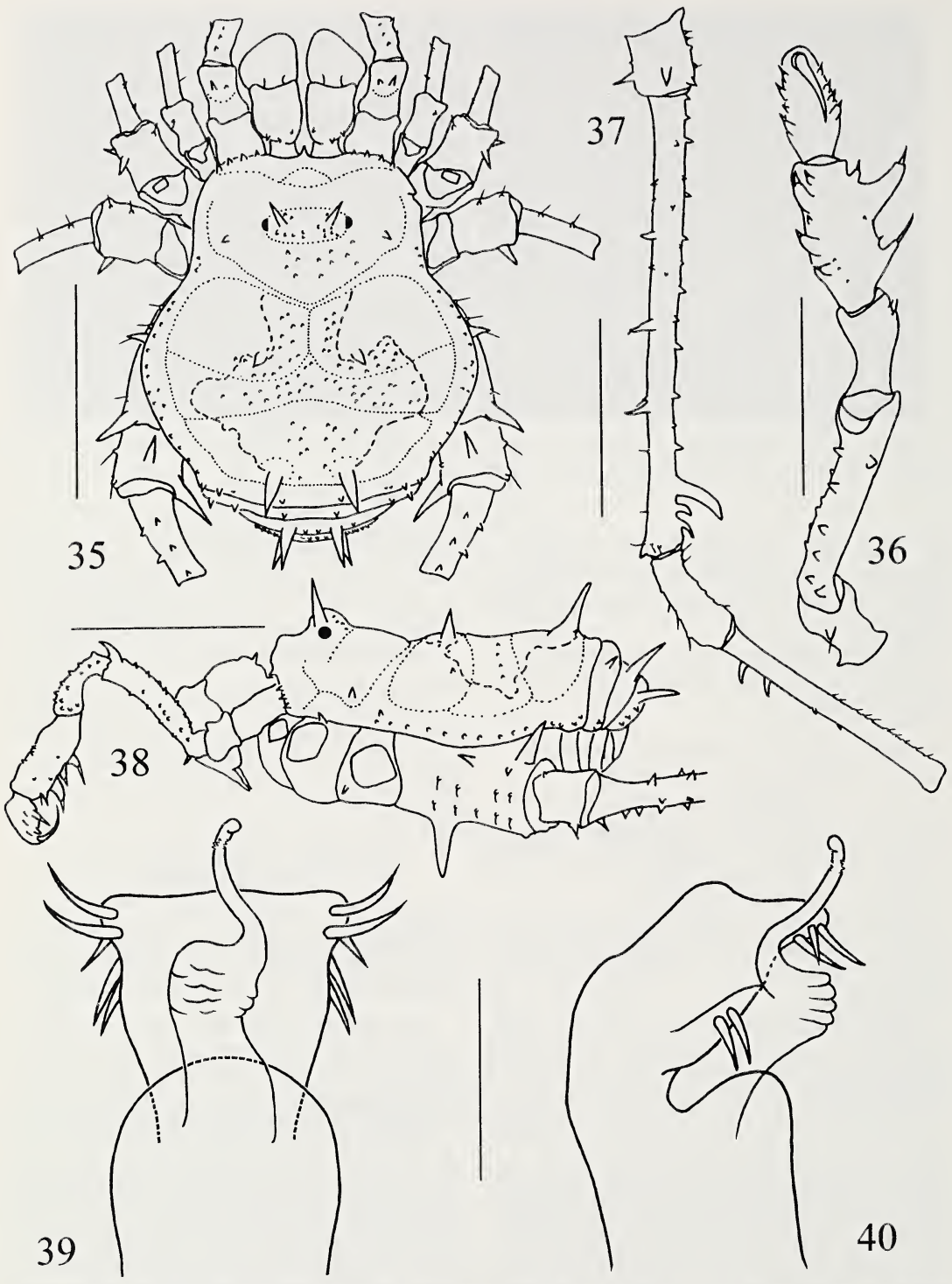
Nieblia festae Roewer 1925: 28, figs. 21 a–b; Soares & Soares 1948: 611 (types ZMT, 1 male, 1 female syntypes, not examined).

Type locality (Fig. 48).—ECUADOR: [Pichincha. San José de] Niebli (ca. 00°10′N, 79°15′W).

Diagnosis.—Anterior margin smooth. Cephalothorax after eye mound with one row of tubercles. Area II with one row of 6 tubercles. Coxa IV without lateral large tubercles. Trochanter IV without dorsal large tubercle. Dorsal scute dark-brown. Distinguished from *S. arthrocentrica* by the concolor pattern of scute and the absence of pointed tubercles of coxa IV of male.

Santinezia curvipes species group

Diagnosis.—Paramedian spines of scutal area III small (except in *S. magna*) (character



Figures 35–40.—*Santinezia arthrocentrica* (Mello-Leitão 1943), male holotype from Macachi (MNRJ 5004): 35. Habitus, dorsal view; 36. Left pedipalpus, ventral view; 37. Right leg IV trochanter to tibia, dorsal view; 38. Habitus, lateral view; 39. Distal part of penis, dorsal view; 40. Same, lateral view. Scale bars = 5 mm (Figures 35–38), 0.10 mm (Figures 39–40).

1, state 1) [A]. Basal group of setae of ventral plate five, forming two nearly transverse rows (character 11, state 1) [A]. General shape of ventral plate guitar-shaped (character 13, state 1) [A]. Tibia IV of male with mesal row occupying proximal half formed by 8–12 spines oblique backwards and which size decreases apically as in *S. serratotibialis*. This row displaced distally in *S. heliae* and *S. calcartibialis* (character 21, states 1 and 2) [A]. Tibia IV of male without two-three ventro-mesal short spines in basal fourth, the most proximal hook-shaped curved (character 23, state 0) [P]. Femur IV of male with 3–7 very small clustered spines, apical to the main spine (excepted in *S. duranti*) (character 25, state 1) [A]. Femur IV of male without submedial mesal apophysis (character 28, state 0) [P]. Pedipalpal femur of male incrassate, strongly convex dorsally (character 32, state 0) [P]. Armature of area III and tibia IV of male promptly allows distinguishing it from the other *Santinezia* species groups.

Male genitalia: Ventral plate with distal border slightly concave, lateral borders also concave especially distally, giving a guitar shape to the plate. With four groups of setae: 3 large lanceolate latero-basal, 2 short dorsal, two short latero-distal and 1–2 large spatulate latero-distal. Dorsal process of glans very small or absent. Stylus widely curved forming a half circle parting from ventro-apical part of glans, opening to ventral side, not bent in apex, not swollen, with small papillae, without stylar apophysis.

Included species.—*Santinezia calcarfemoralis* (Roewer 1916), *Santinezia calcartibialis* (Roewer 1915), *Santinezia circumlineata* González-Sponga 1989, *Santinezia curvipes* (Roewer 1916), *Santinezia duranti* González-Sponga 1989, *Santinezia furva* new species, *Santinezia heliae* Avram 1983, *Santinezia magna* Goodnight & Goodnight 1942, *Santinezia serratotibialis* Roewer 1932, *Santinezia simonbolivari* Avram 1987 and *Santinezia spinulata* Goodnight & Goodnight 1943.

Combined distribution.—COLOMBIA. GUYANA: Essequibo. TRINIDAD & TOBAGO: Tobago; Trinidad. VENEZUELA: Anzoátegui, Aragua, Distrito Federal, Falcón, Miranda, Monagas, Sucre, Zulia.

Santinezia calcarfemoralis (Roewer 1916)
(Fig. 50)

Inezia calcarfemoralis Roewer 1916: 151, fig. 42 (type SMF, male holotype, not examined).

Santinezia calcarfemoralis: Roewer 1923: 554, fig. 692; Roewer 1932: 290; Soares & Soares 1948: 617.

Type locality (Fig. 50).—VENEZUELA: *Zulia:* between Maracaibo and Sierra de Perijá (ca. 10°13′N, 72°23′W).

Diagnosis.—Femur IV slightly curved, male with a large ventral tubercle. Tibia IV straight, without large tubercles. Free tergite I without spines. Sulci and margins of dorsal scute without white stripes. Tarsal segmentation on male: 8, 18, 10, 12. Compared to the species of the curvipes group without any white stripe on scutal grooves; *S. magna*, *S. circumlineata*, *S. serratotibialis*, *S. spinulata.* The absence of mesal row of spines on tibia IV of male is shared only with *S. curvipes*, which, however, possesses white stripes on grooves. Also the chelicerae of male appear to be swollen in this species, much more than any *Santinezia*, which in general do not possess this kind of dimorphism.

Santinezia calcartibialis (Roewer 1915)
(Fig. 51)

Inezia calcartibialis Roewer 1915: 110, fig. 60 (types SMF male and female syntypes, not examined).

Santinezia calcartibialis: Roewer 1923: 553, fig. 691; Roewer 1932: 290; Soares & Soares 1948: 617.

Chondrocranaus scriptus Roewer 1932: 341, fig. 58; Soares & Soares 1948: 592 (type SMF RII 1424/35, female holotype, not examined). NEW SYNONYMY.

Type localities (Fig. 51).—Of both species: VENEZUELA: *Mérida:* Mérida, 3000 m (08°36′N, 71°08′W).

Diagnosis.—Femur IV straight, with large ventral tubercle on male. Tibia IV S-shaped, male with large retrolateral tubercle. Free tergite I with two large spines. Sulci I–III with two white stripes on lateral part. Tarsal segmentation on male: 9, 13, 9, 10. Compared to the species possessing white stripes on scutal grooves; *S. curvipes*, *S. duranti*, *S. furva*, *S. heliae*. *Sui generis* apophysis of male tibia IV separates it from all others.

Remarks.—In spite of the male genitalia being hitherto unknown, judging from the color pattern of the dorsal scutum, this species is surely a member of the curvipes group. Both names were described from the same locality and there is a high coincidence of color pat-

tern and tubercle distribution on the dorsal scute.

Santinezia circumlineata González-Sponga 1989
(Fig. 51)

Santinezia circumlineatus González-Sponga 1989: 59, figs. 1–9 (types MBSVE 0108, male holotype; MCNC 831 female paratype; GSPC 3 male, 8 female paratypes, not examined).

Type locality (Fig. 51).—VENEZUELA: *Anzoátegui:* Sotillo: Cueva Seca or Cueva de El Encanto (10°08′20″N, 64°31′40″W).

Diagnosis.—Femur IV straight, male with large ventral tubercle. Tibia IV straight, male with one large tubercle on the middle followed by other 11 decreasing in size. Free tergite I without spines. Sulci I–III without white stripes. Tarsal segmentation on male: 8–9, 15–18, 10, 11–12; female 7–8, 15–17, 9–10, 10–12. Compared to the species of the *curvipes* group without any white stripe on scutal grooves; *S. magna*, *S. serratotibialis*, *S. calcarfemoralis*, *S. spinulata*. Closest to *S. serratotibialis* by the presence of white stripes on posterior margin and white arches on lateral areas. It can be distinguished from *S. serratotibialis* by the position of the armature of tibia IV, more displaced distally.

Distribution (Fig. 51).—VENEZUELA: *Monagas:* Caripe, Hierbabuena, near Caripe (10°11′40″N, 63°26′50″W) (González-Sponga 1989).

Remarks.—The specific name has been corrected to conform to the feminine gender of the generic name, according to the International Code of Zoological Nomenclature (1999).

Santinezia curvipes (Roewer 1916)
(Fig. 50)

Inezia curvipes Roewer 1916: 8 (type ZMB 11740, male holotype, not examined).

Santinezia curvipes: Roewer 1923: 553; Roewer 1932: 290; Soares & Soares 1948: 617; Moritz 1971: 195; Avram 1987: 84.

Santinezia albilineata Roewer 1932: 290, fig. 7; Goodnight & Goodnight 1949: 23; Caporiacco 1951: 27; Rambla 1978: 8; Avram 1987: 87; Decu et al. 1987: 34; Rambla & Juberthie 1994: 221 (type ZMB 7468, female holotype, not examined). NEW SYNONYMY.

Goniosoma pavani Muñoz-Cuevas 1972: 28, figs. 1–13 (type repository unknown, presumably MNHN). NEW SYNONYMY.

Santinezia benedictoi Soares & Avram 1981: 95 (type repository unknown, male holotype). NEW SYNONYMY.

Santinezia decui Avram 1987: 86, figs. 16–19 (type ISER, female holotype). NEW SYNONYMY.

Santinezia francourbani Avram 1987: 83, figs. 5–11; Rambla & Juberthie 1994: 221 (type ISER, male holotype, 1 juvenile paratype). NEW SYNONYMY.

Santinezia orghidani Avram 1987: 85, figs. 12–15 (type ISER, female holotype). NEW SYNONYMY.

Type localities (Fig. 50).—Of *S. curvipes*: VENEZUELA: *Distrito Federal:* Caracas (10°30′N, 66°55′W). Of *S. benedictoi*: VENEZUELA: Of *S. orghidani*: VENEZUELA: *Aragua:* Parque Nacional Rancho Grande (H. Pittier) (10°20′00″N, 67°38′20″W). *Santinezia albilineata*: VENEZUELA: *Aragua:* San Casimiro (10°00′N, 66°55′W). *Santinezia decui*: VENEZUELA: *Aragua:* Tiara, 1200 m (10°04′10″N, 67°00′00″W). *Santinezia francourbani*: VENEZUELA: *Miranda:* El Hatillo: Cueva de la Esmeralda, 1120 m (10°19′10″N, 66°48′20″W). *Goniosoma pavani*: VENEZUELA: *Aragua:* Rancho Grande (10°20′00″N, 67°38′20″W).

Records.—VENEZUELA: *Aragua:* National Park of Aragua, Rancho Grande (Goodnight & Goodnight 1949).

False records.—*Falcón:* Valle Acarite, Cueva Zárraga 900 m (Decu et al. 1987). This record refers to *S. heliae*, as determined by Avram (1987).

Material examined.—VENEZUELA: *Miranda:* 1 ♂, 1 ♀, Guatopo National Park, Santa Cruzita (10°06′10″N, 66°24′20″W), 13 February 1984, J. Coddington (USNM); 1 immature, Agua Blanca, 450 m, 13 February 1984, J. Coddington (USNM); 1 ♂, 1 ♀, same data (MZSP); 1 ♀, along highway 12 Sur, 1.4 km from Los Alpes (about 10°04′N 66°28′W), in secondary growth bordering forest, 600 m, 25 April 1991, C. Roesel (USNM); 2 ♂, 4 ♀ 1 immature, Birongo, outside Cueva Alfredo Jahn, 270 m (10°08′20″N, 63°38′20″W), 15 February 1984, J. Coddington (USNM); *Aragua:* 3 ♂, 3 ♀, Parque Nacional Henri Petier, Rancho Grande, 17 October 1966, S.S. & W.D. Duckworth (USNM); 2 ♀, same data, 20 February 1969, P. & Spangler (USNM); same data, 18 February 1984, J. Coddington (USNM); 1 ♀, 3 km N Rancho Grande, 750 m, February 1987, E.S. Ross (CAS); 2 ♀,

Henri Pittier Nat. Park, Pico Periquito, 1680 m, malaise trap, 15–30 November 1997, T. Pape (NRMS); 3 ♂, 3 ♀, Henri Pittier Nat. Park, near Rancho Grande, 1100–1800 m, 12–30 November 1997, T. Pape, (NRMS); 2 ♂, 1 ♀, same data (MNRJ 5606); 2 ♀, Rancho Grande, 8–11 June 1976, A.S. Menke & D. Vincent (USNM); *Distrito Federal:* 3 ♂, 1 ♀, Caracas, Hac. La Trinidad, shallow cave, 1500 m, 28 December 1970, W. B. Peck (CAS).

Diagnosis.—Femur IV slightly curved, male with large ventral tubercle. Tibia IV straight, with large tubercles. Free tergite I without spines. Sulci I–II with wide white stripe. Tarsal segmentation on male: 8, 21, 9–10, 12; ♀ 8, 17, 9, 10. Compared to the species possessing white stripes on scutal grooves; *S. calcartibialis*, *S. duranti*, *S. furva*, *S. heliae*. Distinguished from all by the apophysis of coxa IV of male oblique backwards.

Remarks.—The type material of *S. albilineata* has not been cited in the catalog of ZMB opilionid types (Moritz 1971). Our request to ISER (Dr V. Decu) of type material of the species described by Avram went unanswered. This material is presumably lost.

This species has been described many times, all but once in the genus *Santinezia*. The characters used to separate species of this genus were basically the row of lateral tubercles in the lateral margins of the scutum, the pattern of white marks on the dorsal scutum and the curvature of femur IV of the male, all these characters are highly variable and sex-dependent (the first one) or age-dependent (the third one). The descriptions of Soares & Avram (1981) and Avram (1987) are extremely summary and based on very few specimens. The allocation of this species to *Goniosoma* was done due to lack of acquaintance with nothern South American Opiliones. Muñoz-Cuevas specialized in the Chilean fauna, mainly Pachylinae and Triaenonychidae. The species of *Goniosoma*, like *Santinezia*, are also stout long-legged Laniatores with the scutal area II invading area I. They are, however, typical Gonyleptidae, and the male genitalia are completely different from those of the Cranaidae.

Santinezia duranti González-Sponga 1989
(Fig. 50)

Santinezia duranti González-Sponga 1989: 64, figs. 10–19 (types MBSVE 0398 male holotype; GSPC male paratype, not examined).

Type locality.—VENEZUELA: *Monagas:* Caripe (10°11′40″N, 63°26′50″W): Sima de la Montaña.

Records (Fig. 50).—VENEZUELA: *Monagas:* Caripe: Cueva Morocoima (10°18′20″N, 63°26′40″W) (González-Sponga 1989).

Diagnosis.—Femur IV straight, male with large ventral tubercle. Tibia IV straight, male with one subdistal row of 13 tubercles decreasing in size. Free tergite I with one pair of spines. Sulci I–III and posterior margin with two lateral white stripes. Tarsal segmentation on male: 10, 21–23, 10–12, 13. Compared to the species possessing white stripes on scutal grooves; *S. calcartibialis*, *S. curvipes*, *S. furva*, *S. heliae*. Absence of sui generis apophysis of male tibia IV, apophysis of coxa IV of male straight and absence of mesal sub apical spine in pedipalpal femur relate it to *S. heliae*. Separated by granulation of scute and tergites, armature of tibia IV and white spot on carapace.

Santinezia furva new species
(Figs. 41–45, 51)

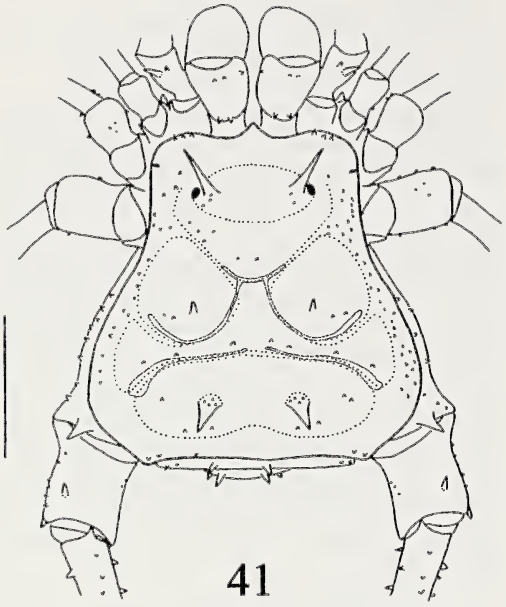
Type locality (Fig. 51).—VENEZUELA: *Zulia:* Sierra de Perijá, Mesa Turik (10°45′N, 72°30′W), Depresión de Euskalpiça, Cueva del Fiambre.

Material examined.—Male holotype: VENEZUELA: *Zulia:* Cueva del Fiambre, 19 March 1991, Joris Lagarde (MBUZ). Paratype: COLOMBIA: *Magdalena:* 1 ♀, Sierra de Perijá: Finca San José, 8 km SE of Socorpa Mission, 1450–1500 m, 27–31 July 1968, B. Malkin (AMNH).

Etymology.—From Latin, furva for black, because of the color of the body and appendages.

Diagnosis.—Femur IV straight, male with large ventral tubercle. Tibia IV straight, male with large ventro-subbasal tubercle. Free tergite I with one pair of spines. Sulci II–III with two wide white stripes. Tarsal segmentation on male: 9–10, 19, 11, 10–12. Compared to the species possessing white stripes on scutal grooves; *S. calcartibialis*, *S. curvipes*, *S. duranti*, *S. heliae*. Distinguished by the presence of mesal sub apical spine in pedipalpal femur.

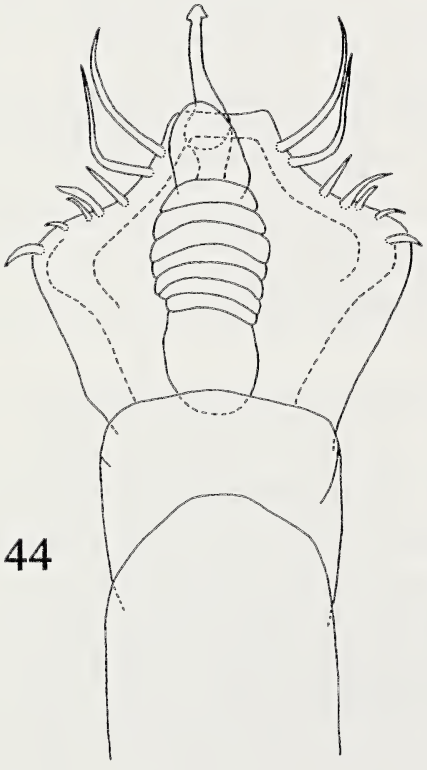
Description.—Male holotype: Measurements (mm): Dorsal scute length 10.8; width 10.5; cephalothorax length 4.9; width 6.5; pedichpalpal femur 5.2; femur IV 30.5; leg I 40; II 78; III 60; IV?. Dorsal scutum (Fig. 41):



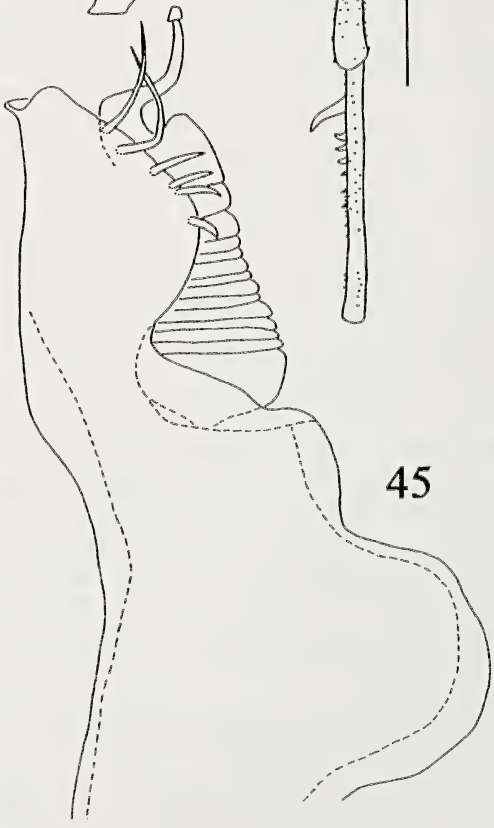
41

42

43



44



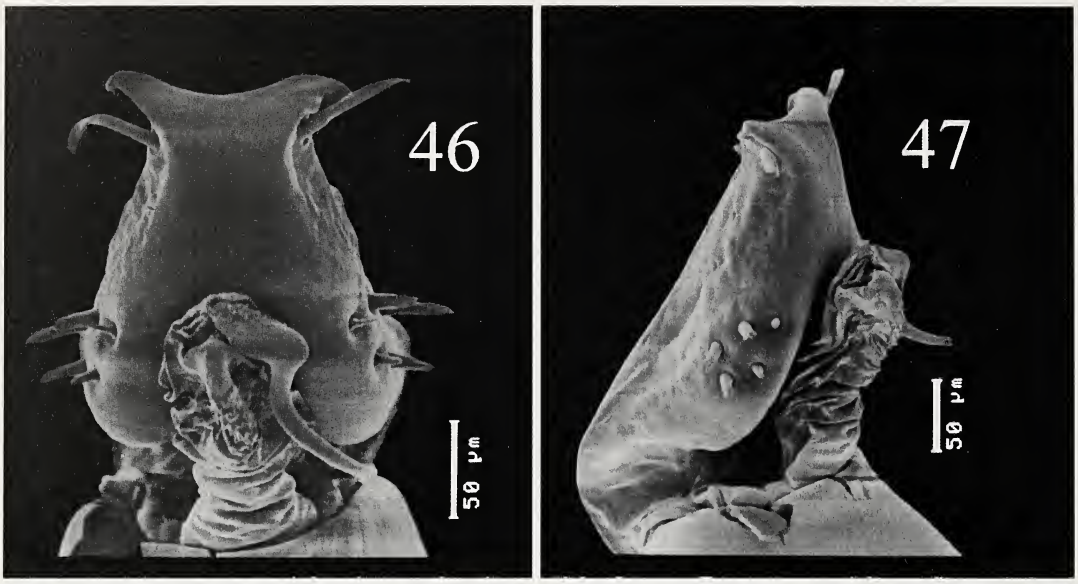
45

Anterior border with three lateral tubercles on each side. Eye mound with two sharp high spines, five posterior tubercles. Carapace with nine tubercles behind eye mound and one to three beside. Area I with three tubercles in each half (median larger); area II with seven tubercles; area III with two spines with tuberculate basis. Posterior border with two tubercles on each side. Free tergites I–III with pair of median high tubercles; I with three small tubercles on each side; II–III with two small tubercles on each side. Anal operculum with small tubercles irregularly arranged. Venter: Coxa I with median row of six tubercles, four anterior, three posterior, five apical; coxa II with median row of seven tubercles, five anterior, five apical; coxa III with median row of eight tubercles, seven anterior, eight posterior, five apical; coxa IV with two transverse rows of tubercles, others irregularly arranged; one pair of low apophyses near the stigmata. Ventral anal operculum with low setiferous tubercles. Chelicera: Basichelicerite with three anterior and two long posterior tubercles; hand with two frontal rows of tubercles one with 10–12 and the other with 5–6; fixed finger with three teeth; movable finger with four teeth. Pedipalpus (Fig. 42): Coxa with two ventral tubercles. Trochanter with three ventral tubercles, 2–3 dorsal (1 longer). Femur with 10–12 retrolateral tubercles, 8–9 dorsal (apical long); one ventrobasal bifid tubercle; two ventral rows of five and six tubercles. Patella and tibia granular dorsally. Tibia with four mesal (IiIi) and four ectal (IiIi) socketed spines. Tarsus, with five mesal (iIiIi) and five ectal (iIiIi) socketed spines. Legs (Fig. 43): Trochanter I–III with many small dorsal tubercles; I–II with four ventral high tubercles; III with six ventral, one retrolatero-apical, one prolatero-apical; IV with one long retrolateral, one long dorsal, five prolateral, four retrolateral and 10 ventral tubercles. Femora I–IV straight; IV with one ventral subapical long curved tubercle and two rows with 3–4 smaller tubercles. Patella IV irregularly tubercled. Tibia IV with one subbasal apophysis strongly curved, followed by row of 12 tubercles decreasing in size. Tarsal articles: 9–10/19/11/10–12. Distitarsi I–II with 3 articles. Male genitalia (Figs. 44–45): Ventral plate with distal border slightly concave, lateral borders also concave especially distally, giving to the plate a guitar shape. Distal corners not projected. With two groups of setae: five lanceolate latero-basal and two sinuous latero-distal with distal third spatulate. Glans with very small dorsal process. Stylus arising straight from glans. Apex not bent, but a bit swollen, with small papillae, without stylar apophysis. Color: Body background and legs dark brown. Carapace reticled in black. Groove I with short white median stripe; II with white stripe along its extension; III with two long white stripes. Scutum with light brown stripes from groove I–IV; area I with round light brown spot. Free tergite III with white stripe between tubercles.

Female paratype (AMNH): Measurements (mm): Dorsal scute length 9.9; width 9.9; cephalothorax length 4.2; width 6.1; pedipalpal femur 4.9; femur IV 22; leg I 34; II 74; III 54; IV 71. Anterior margin of carapace with two tubercles each side. four posterior setiferous tubercles each side behind eye mound. Eye mound smooth around spines. Area I with a transverse row of four tubercles on each half, the second much stouter; area II with a row of eight setiferous tubercles in the middle; area III with two sharp parallel high spines, and two external and one posterior setiferous tubercle on each side. Free tergites I–III each with two high spines and 3–4 external small setiferous tubercles. Chelicera: coxa (basichelicerite) with meso-apical stout setiferous tubercle; bulla of basichelicerite with four tubercles on posterior margin, the outermost much stouter; hand with one longitudinal frontal row of subequal tubercles; fixed finger with four teeth broad low and movable finger with two. Pedipalpus: trochanter with four ventro-apical tubercles, one much stouter; femur with ventral row of eight tubercles and a ventro-mesal basal stout spine, dorsal row of

←

Figures 41–45.—*Santinezia furva* new species, male holotype from Cueva del Fiambre (MBUZ): 41. Habitus, dorsal view; 42. Left pedipalpus, ventral view; 43. Right leg IV trochanter to tibia, dorsal view; 44. Distal part of penis, dorsal view; 45. Same, lateral view. Scale bars = 5 mm (Figs. 41–43), 0.10 mm (Figs. 44–45).



Figures 46–47.—*Santinezia serratotibialis* Roewer 1932, male from Santa Simla (HSPC 1061): 46. Distal part of penis, dorsal view; 47. Same, lateral view. Scale bars = 0.05 mm.

eight granules and a dorso-apical spine; tibia with four mesal (IiIi) and four ectal (IiIi) and tarsus with four mesal (IiIi) and five ectal (iIiIi) socketed spines. Coxa IV with apical spiniform apophysis; trochanter IV with dorso-median, prolateral and retrolatero-apical spiniform apophyses. Tarsal articles: 9/17–18/10/11. Distitarsi I–II with three segments. All tarsi hirsute ventrally. Body background dark brown, a little lighter in metatarsi and tarsi, much darker in free tergites and lateral margins. Grooves I–III lined in white.

Santinezia heliae Avram 1983
(Fig. 50)

Santinezia heliae Avram 1983: 15; Avram 1987: 81; González-Sponga 1989: 70, figs. 20–28 (types MBSVE, male holotype, 2 male, 3 female paratypes, not examined).

Type locality (Fig. 50).—VENEZUELA: *Falcón:* Curimagua: Cueva San Juan de Lugo, 1000 m (11°04′10″N, 69°38′20″W); La Dolorita; Cabure: Cueva Hueque 3 (11°10′50″N, 69°35′00″W).

Diagnosis.—Femur IV straight, male with large ventral tubercle. Tibia IV straight, male with large retrolateral tubercle on middle. Free tergite I with one pair of spines. Sulci I–III with two wide white stripes. Tarsal segmentation on male: 8–9, 15–18, 9–10, 9–11. Compared to the species possessing white stripes on scutal grooves; *S. calcartibialis*, *S. curvipes*, *S. duranti*, *S. furva*. Absence of sui generis apophysis of male tibia IV, apophysis of coxa IV of male straight and absence of mesal sub apical spine in pedipalpal femur relate it to *S. duranti*. Separated by granulation of scute and tergites, armature of tibia IV and absence of white spot on carapace.

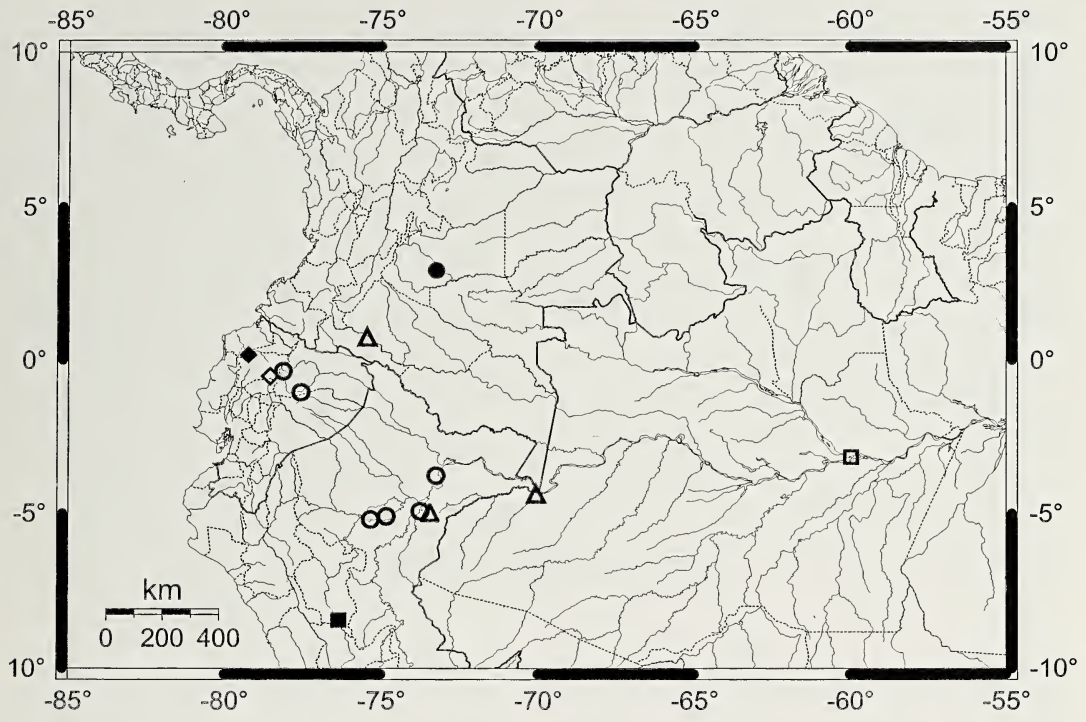
Records (Fig. 50).—VENEZUELA: *Falcón:* Acosta: Sierra de San Luís, Cueva del Tigre (11°10′00″N, 68°43′20″W) (Avram 1983). *Falcón:* Curimagua, Valle Acarite: Cueva Zárraga, 900 mm (11°04′10″N, 69°38′20″W) (Avram 1987).

Santinezia magna Goodnight & Goodnight 1942
(Fig. 51)

Santinezia magna Goodnight & Goodnight 1942: 8, fig. 20; Soares & Soares 1948: 618 (type AMNH, male holotype, not examined).

Type locality (Fig. 51).—GUYANA: *Essequibo:* Tukeit.

Diagnosis.—Femur IV with large subdistal tubercle. Free tergite I without spines. Posterior and lateral margin with one wide white stripe. Male tarsal segmentation: 9, 23, 12, 14. Compared to the species of the *curvipes* group without any white stripe on scutal grooves; *S. circumlineata*, *S. serratotibialis*, *S. calcarfemoralis*, *S. spinulata*. This species is much



48

Figure 48.—Western South America showing distribution of species of *Santinezia* groups *festae* and *gigantea*. ♦ = *S. festae*; ◊ = *S. arthrocentrica*; ■ = *S. ortizi*; = *S. angelica*; ○ = *S. hermosa*; Δ = *S. singularis* and □ = *S. manauara*.

imperfectly known. Lack of accessory ectoapical spines of femur IV of male separates it from all others.

Records (Fig. 51).—GUYANA: *Essequibo:* Kaieteur [Falls] (05°11′30″N, 59°29′00″W).

Santinezia serratotibialis Roewer 1932
(Figs. 46, 47, 51)

Santinezia serratotibialis Roewer 1932: 291, fig. 8; Soares & Soares 1948: 618 (types BMNH 6974, 3 male, 1 female syntypes, not examined).

Santinezia biordi González-Sponga 1991: 200, figs. 19–28 (types MAGS 945a male holotype; MAGS 945b female paratype). NEW SYNONYMY.

Type localities (Fig. 51).—Of *S. serratotibialis*: TRINIDAD (wrongly cited as BOLIVIA: "Trindade" in the original description). Of *S. biordi*: VENEZUELA: *Sucre:* Arismendi: Uquire, Parque Nacional "Península de Paria" (10°42′10″N, 61°59′20″W).

Material examined (Fig. 51).—TRINIDAD & TOBAGO: *Tobago:* 1♂, St. Paul Parish, King's Bay R. Dam, 1.2 mi SW of Speyside, 290 m, 10–17 May 1991, G. Hormiga & S. Larcher (USNM); 10♂, 13♀, 1 juvenile, Charloteville, 14–21 March 1979, D. Hardy & W. Rowe (USNM); 4♂, 2♀, same data (MNRJ 5509). *Trinidad:* 1♂, 4 mi N Arima road to Blanchisseuse Rd, W. Beebe—Reserva Tropical Santa Simla, 13 December 1978, A. L. Brawell & D. L. Stephan (HSPC 1061); St. Paul: 1 ♂, 2 ♀, 1 juvenile, Merchiston, Jane Boyle property, 23 December 1978, A.L. Braswell & D.L. Stephan (HSPC 1062); 3 ♂, 12 ♀, Telecommunications System of Trinidad & Tobago (TSTT) tower between 9 & 10 mile posts of Blachisseuse Road about 10 km N Arima 13–21 September 1996, R.G. Holmberg, E. Fuller & T. Thormin (MNRJ 4630).

Diagnosis.—Male femur IV and tibia IV straight, femur with one large subdistal tubercle, tibia with one ventral row of 15 tubercles decreasing in size. Free tergite one without spines. White stripes on posterior and lateral margins. Male tarsal segmentation: 8–9, 18–22, 10–12, 11–13. Compared to the species of

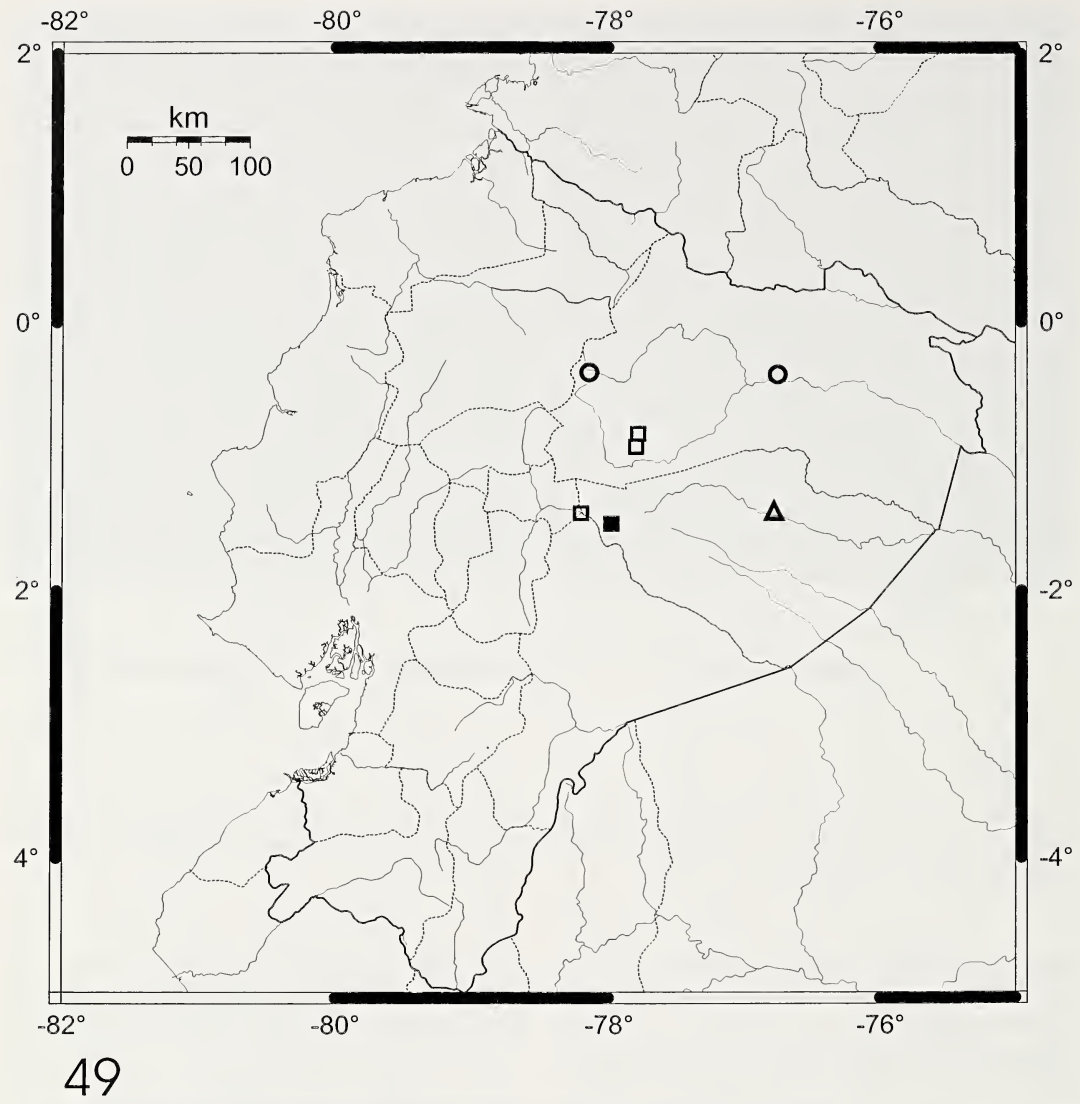


Figure 49.—Northeastern Ecuador showing (continued) distribution of species of *Santinezia* group *gigantea*. Δ = *S. onorei*; □ = *S. gigantea*; ■ = *S. lucifer* and ○ = *S. gracilis*.

the *curvipes* group without any white stripe on scutal grooves; *S. magna*, *S. circumlineata*, *S. calcarfemoralis*, *S. spinulata*. Closest to *S. circumlineata* by the presence of white stripes on posterior margin and white arches on lateral areas. It can be distinguished from *S. circumlineata* by the basal position of the spine comb in tibia IV.

Remarks.—Roewer (1932) described this species as from Bolivia, which surely led González-Sponga not to include it in the suppositions of close relatives when identifying the deemed new species *S. biordi*. The single difference between *S. biordi* and the abundant material we examined is the number and position of ventral setae in the ventral plate of the penis, surely an important diagnostic character. In this case we believe that the setae of González-Sponga's drawing are innaccurate, especially because they are not all in the same plane and are easily overlooked in the optical microscope.

Supplementary description.—*Male genitalia* (Figs. 46, 47)*:* Ventral plate with distal border slightly concave, lateral borders also concave especially distally, giving to the plate a guitar shape. Distal corners projected as recurved lobes. With two groups of setae: five

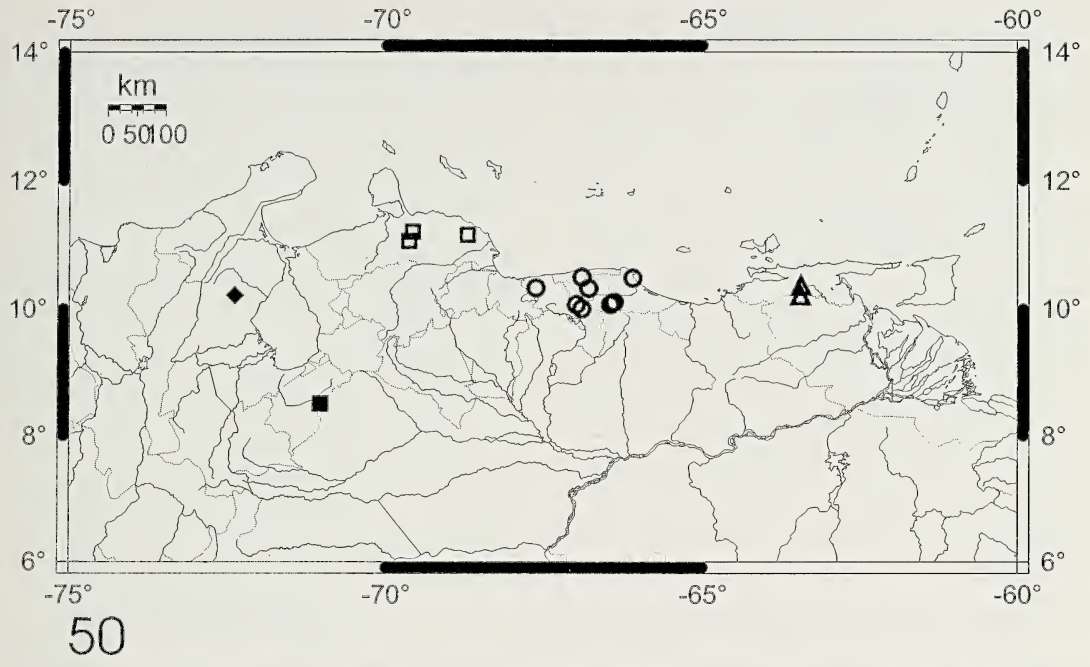


Figure 50.—Eastern Colombia and northwestern Venezuela, showing distribution of species of *Santinezia* group *curvipes*. ♦ = *S. calcarfemoralis*; ■ = *S. simonbolivari*; □ = *S. heliae*; ○ = *S. curvipes* and Δ = *S. duranti*.

lanceolate latero-basal and one sinuous latero-distal with distal third spatulate. Glans with very small dorsal process. Stylus arising straight from glans. Apex not bent, but a bit swollen, with small papillae, without stylar apophysis.

Santinezia simonbolivari Avram 1987
(Fig. 50)

Santinezia simonbolivari Avram 1987: 81, figs. 1–4 (type repository unknown, female holotype, not examined).

Type locality (Fig. 50).—VENEZUELA: *Mérida:* La Mucuy, Tabay, 2300 m (08°30′50″N, 71°01′40″W).

Remarks.—In spite of males being unknown, judging from the color pattern of the dorsal scutum, this species is surely a member of the curvipes group. A precise diagnosis for females of this group is impossible at this moment due to the weak variation of this sex.

Santinezia spinulata Goodnight & Goodnight 1943
(Fig. 51)

Santinezia spinulata Goodnight & Goodnight 1943: 9, figs. 26–28; Soares & Soares 1948: 618 (types AMNH, male and female syntypes, not examined).

Type locality (Fig. 51).—COLOMBIA. No other data.

Diagnosis.—Femur IV straight, with a long ventral tubercle on male. Tibia IV straight, with a decreasing in size row of straight tubercles on basal half. Free tergite I without spines. Sulci I–III and margins of dorsal scute without white stripes. Male tarsal segmentation counts: 9, 18, 9, 10. Compared to the species of the curvipes group without any white stripe on scutal grooves; *S. magna*, *S. circumlineata*, *S. serratotibialis*, *S. calcarfemoralis*. This species is poorly known. Like *S. magna* and *S. calcarfemoralis* it has the scute entirely uniform, without white stripes in lateral areas and posterior margin. Well developed femoral spines in leg IV separate it from *S. magna* and chelicerae non dimorphic separate it from *S. calcarfemoralis*. Also distinguished from both by the presence of inner subapical spine in pedipalpal femur.

DISCUSSION

The species known only by females are not included in the phylogenetic analysis, and are

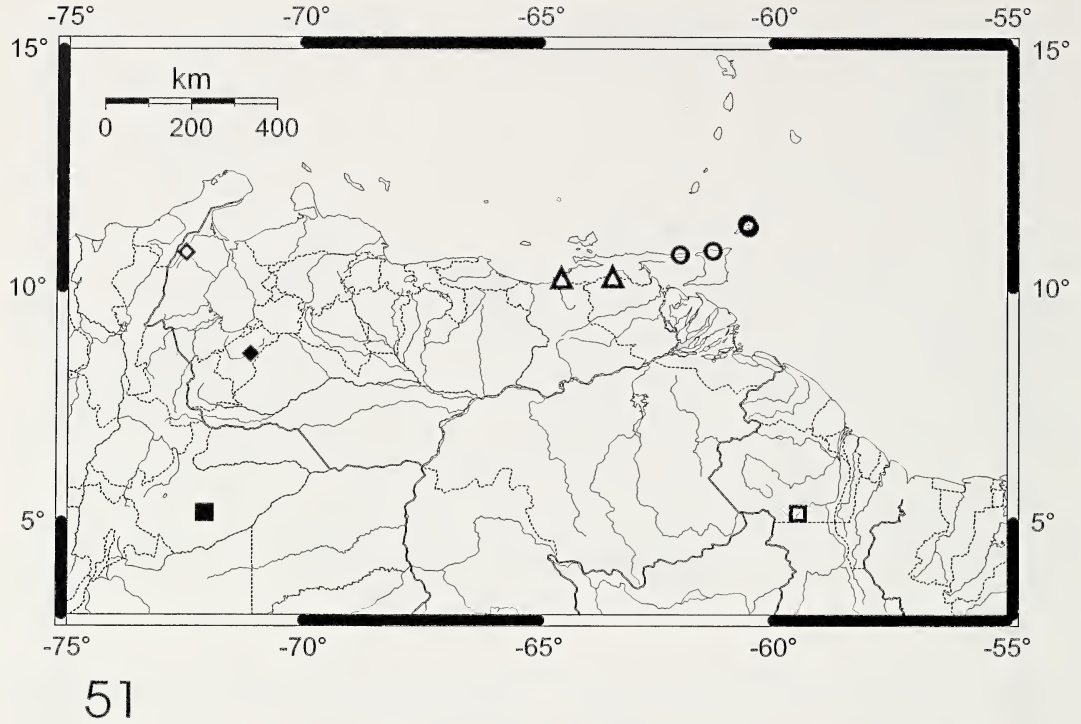


Figure 51.—Eastern Colombia and northwestern Venezuela, showing distribution of species of *Santinezia* group *serratotibialis*. ■ = *S. spinulata*; ◇ = *S. furva*; ◆ = *S. calcartibialis*; Δ = *S. circumlineata*; ○ = *S. serratotibialis* and □ = *S. magna*. Accurate spot of type locality of *S. spinulata* is unknown.

only tentatively included in the four species groups defined above. Many Venezuelan species (Avram 1983, 1987; Soares & Avram 1981) were based solely on females and were poorly described. Others await further work to determine if they really constitute distinct species. The genus *Carvalholeptes* has been erected for the species *Carvalholeptes singularis* from Brazilian Amazonia. This species shares many derived traits with the gigantea group of *Santinezia*. The base for the creation of this monotypic genus by Helia Soares was not recognizing the diagnostic characters of *Santinezia*, mainly the ventral apophysis in coxa IV, which this author mistakenly considered to be in the stigmatic area. The equally monotypic *Macuchicola* is related to the type species of *Nieblia*. The other two species of *Nieblia* do not belong to *Santinezia*.

There are a dozen species currently included in *Phareicranaus*, ranging in western South America from Chile to Colombia. The two species of *Nieblia* other than the type are known only from females, making it presently impossible to distinguish them from *Phareicranaus* or *Santinezia*. The pattern of sulfur yellow granules of mesotergum presented by these species is typical of many species of *Phareicranaus*, so they are herein tentatively allocated to this genus.

ACKNOWLEDGMENTS

We are indebted to Drs. Norman Platnick (AMNH), Charles Griswold (CAS), Torbjorn Kronestedt (NRMS), Herbert Levi and Laura Leibensperger (MCZ), Diana Silva D. and Gerardo Lamas (MUSM), Giovanni Onoré (PUCQ) and Jonathan Coddington (USNM) for the loan of material. This study has been supported by grant # 300175/94-9 from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) to ABK and grant # 94/1307-0 from FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) to RPR. The SEM micrographs were taken at the Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo through the kindness of Dr Alberto A.G.F.C. Ribeiro and Mr Márcio Cruz.

LITERATURE CITED

Ab'Saber, A N. 1977. Os Domínios Morfoclimáticos da América do Sul. Geomorfologia 52:1–21.

Avram, S. 1973. Recherches sur les opilionides de Cuba. I. Phalangodidae. Description de *Jimeneziella* n.g., de *J. decui* n.sp. et de *J. negreai* n.sp. Resultats Expeditions biospeleologiques cubano-roumaine a Cuba 1:243–249.

Avram, S. 1983. Gonyleptidae nouveaux du Vénézuéla et du Pérou (Opiliones: Gonyleptomorphi). Boletin Sociedad Venezuelana Espeleologia 20: 11–18.

Avram, S. 1987. Opilionides du Venezuela IV. Fauna hipogea y hemiedafica de Venezuela y de otros paises de América del Sur 1(8):81–88.

Brown, F.M. 1941. A gazetteer of entomological stations in Ecuador. Annals of the Entomological Society of America 34:809–851.

Butler, A.G. 1873. A monographic list of the species of the genus *Gonyleptes* with descriptions of three remarkable species. Annals and Magazine of Natural History 11(4):112–117.

Caporiacco, L. di. 1951. Studi sugli Aracnidi del Venezuela racolti dalla sezione di Biologia (Universitá Centrale del Venezuela). I parte: Scorpiones, Solifuga, Opiliones e Chernetes. Acta Biologica Venezuelana 1(1):1–46.

Decu, V., C. Bordon & O. Linares. 1987. Las estaciones de América del Sur de donde ha sido colectado el material zoológico que está en presente en estudio en el Instituto de Espeleología de Bucarest (Rumanía). Situación del material. Fauna hipogea y hemiedáfica de Venezuela y de otros paises de América del Sur 1:29–45.

Farris, J.S. 1988. Hennig86, version 1.5. Computer program and documentation. Port Jefferson Station, NY.

Goloboff, P.A. 1993a. Pee-Wee Ver. 1.96 documentation. New York, N.Y.

Goloboff, P.A. 1993b. Estimating character weights during tree search. Cladistics 9(1):83–91.

González-Sponga, M.A. 1989. Dos especies nuevas de opiliones del genero *Santinezia* de Venezuela y redescripcion de *Santinezia heliae* Avram 1983. Boletin Academia Ciencias Fisicas y Naturales de Caracas 49(155–156):57–77.

González-Sponga, M.A. 1991. Arácnidos del Parque Nacional "Península de Paria", en Venezuela (Opiliones: Laniatores). Boletin Academia Ciencias Fisicas y Naturales de Caracas 50:185–210.

Goodnight, J.C. & M.L. Goodnight. 1942. Phalangids from British Guiana. American Museum Novitates 1167:1–13.

Goodnight, J.C. & M.L. Goodnight. 1943. Phalangida from South America. American Museum Novitates 1234:1–19.

Goodnight, J.C. & M.L. Goodnight. 1947. Studies on the phalangid fauna of central America. American Museum Novitates 1340:1–21.

Goodnight, J.C. & M.L. Goodnight. 1949. Report on a collection of phalangids from Rancho Grande, Venezuela. Zoologica, New York 34:21–24.

International Commision on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth Edition. International Trust for Zoological Nomenclature, London.

Kästner, A.. 1937. Chelicerata 7. Ordnung der Arachnida: Opiliones Sundeval Weberknechte. Pp. 300–393. *In* W. Kukenthal & T. Krumbach, editors, Handbuch der Zoologie. Vol. 3, no. 2. Walter de Gruyter & Co., Berlin & Leipzig.

Kury, A.B. 1994. The genus *Yania* and other presumed Tricommatidae from South American highlands (Opiliones, Cranaidae, Prostygninae). Revue Arachnologique 10(7):137–145.

Kury, A.B. 1997. The genera *Saramacia* and *Syncranaus* Roewer, with notes on the status of the Manaosbiidae (Opiliones, Laniatores, Gonyleptoidea). Boletim Museu Nacional Rio de Janeiro 374:1–22.

Mello-Leitão, C.F. de. 1926. Notas sobre Opiliones Laniatores sul- americanos. Revista Museu Paulista 14:327–383.

Mello-Leitão, C.F. de. 1932. Opiliões do Brasil. Revista Museu Paulista 17(2):1–505.

Mello-Leitão, C.F. de. 1935. Algumas notas sobre os Laniatores. Archivos Museu Nacional Rio de Janeiro 36(4):87–116.

Mello-Leitão, C.F. de. 1939. Dois gêneros e sete espécies de Goniléptidas sulamericanos. Boletim Biologia, nova série 4(3):345–351.

Mello-Leitão, C.F. de. 1942. Oito novos Laniatores do Equador. Annais Academia Brasileira de Ciências 14(4):315–325.

Mello-Leitão, C.F. de. 1943. Arácnidos recogidos en el Ecuador y en el Perú por la señora H.E. Frizell Don. Comunicaciones Zoologicas Museo Historia Natural Montevideo 5(1):1–8.

Mello-Leitão, C. F. de. 1949. Famílias, subfamília, espécies e gêneros novos de opiliões e notas de sinonímia. Boletim do Museu Nacional Rio de Janeiro, nova série 94:1–33.

Moritz, M. 1971. Die Typen der Arachniden-Sammlung der zoologischen Museums Berlin I. Opiliones. Mitteilungen Zoologischen Museum aus dem Berlin 47(1):189–214.

Muñoz-Cuevas, A. 1972. Description de *Goniosoma pavani* n. sp. du Venezuela (Arachn: Gonyleptidae: Goniosominae). Bolletino Sociedad Entomologica Italiana 104:28–32, 13 figs.

Nixon, K. 1992. CLADOS version 1.2 documentation. Cornell University, Ithaca.

Nixon, K.C. & J.M. Carpenter. 1993. On outgroups. Cladistics 9:413–426.

Pinto-da-Rocha, R. 1994. A new species of *Santi-*

nezia from central Amazonia, with systematic comments on the genus (Arachnida, Opiliones, Cranaidae). Andrias 13:29–32.

Rambla, M. 1978. Opiliones cavernicoles de Venezuela. Speleon 24:5–22.

Rambla, M. & C. Juberthie. 1994. Opiliones. *In* C. Juberthie & V. Decu (eds.), Encyclopaedia Biospeologica I:215–230.

Roewer, C.F. 1913. Die Familie der Gonyleptiden der Opiliones-Laniatores. Archiv für Naturgeschichte 79A(4):257–472.

Roewer, C.F. 1915. 106 neue Opilioniden. Archiv für Naturgeschichte 81A(3):1–152.

Roewer, C.F. 1916. 7 neue Opilioniden des Zoolog. Museums in Berlin. Archiv für Naturgeschichte 81A(12):6–13.

Roewer, C.F. 1923. Die Weberknechte der Erde. Sistematische Bearbeitung der bisher bekannten Opiliones. 1116 pp., Gustav Fischer, Jena.

Roewer, C. F. 1925. Opilioniden aus Süd-Amerika. Bolletino dei Musei di Zoologia ed Anatomia Comparata della Universita di Torino, NS 34(40):1–34.

Roewer, C.F. 1932. Weitere Weberknechte VII (7. Ergänzung der Weberknechte der Erde 1923). Archiv für Naturgeschichte aus dem Berlin 1(2): 275–350.

Roewer, C.F. 1952. Neotropische Arachnida Arthrogastra zumeist aus Peru. Senckenbergiana 33(1–3):37–58.

Roewer, C.F. 1963. Opiliones aus Peru und Colombia. [Arachnida Arthrogastra aus Peru V. Senckenbergiana Biologica 44:45–72.

Simon, E. 1879. Essai dune classification des Opiliones Mecostethi remarques synonymiques et descriptions despéces nouvelles. Annales de la Société Entomologique de Belgique 22:183–241.

Soares, B.A.M. & H.E.M. Soares. 1948. Monografia dos gêneros de opiliões neotrópicos I. Arquivos de Zoologia do Estado de São Paulo 5(9): 553–636.

Soares, H.E.M. 1970. Novas espécies de opiliões da Região Amazônica (Opiliones, Cosmetidae, Gonyleptidae, Phalangiidae, Stygnidae). Revta Brasileira Biologia 30(3):323–338.

Soares, H.E.M. & S. Avram. 1981. Opilionides du Venezuela I. Travaux Instutut Spéologie Emile Racovitza 20:75–95.

Manuscript received 7 January 2002, revised 14 August 2002.

2003. The Journal of Arachnology 31:209–245

ON THE USE OF AMPULLATE GLAND SILKS BY WOLF SPIDERS (ARANEAE, LYCOSIDAE) FOR ATTACHING THE EGG SAC TO THE SPINNERETS AND A PROPOSAL FOR DEFINING NUBBINS AND TARTIPORES

Mark A. Townley and **Edward K. Tillinghast**: Department of Zoology, Rudman Hall, University of New Hampshire, Durham, New Hampshire 03824 USA. E-mail: mtownley@cisunix.unh.edu

ABSTRACT. The means by which female wolf spiders attach an egg sac to their spinnerets was investigated using scanning electron microscopy. In four *Pardosa* species, we observed that silk fibers emerging from ampullate gland spigots had been affixed to the surface of the egg sac. More specifically, primary (1°) and secondary (2°) major ampullate (MaA) glands and 1° and 2° minor ampullate (MiA) glands all contributed fibers for this purpose. The diameters of the 2° MaA and 2° MiA fibers were greater than those of the 1° MaA and 1° MiA fibers and, correspondingly, the widths of the 2° ampullate spigots were clearly greater than those of the 1° ampullate spigots. Larger 2° ampullate spigots were also observed in adult females of species from three other lycosid genera. Thus, 2° ampullate glands, which in araneoids function only in juveniles during proecdysis, are not only functional in adult female lycosids (and adult females of several other families), but they appear to play a greater role than the 1° ampullate glands in egg sac attachment. Observations made on the 1° and 2° ampullate spigots of adult females from species belonging to several other families are also presented. Cuticular structures referred to as nubbins and tartipores are present in some spinning fields on spinnerets. A proposal is made for defining these terms by a criterion, namely their different origins, which differs from that applied previously.

Keywords: Ampullate silk gland, *Pardosa*, *Hogna*, *Trochosa*, Lycosoidea

With some exceptions, those spiders that typically carry their egg sacs using only their spinnerets belong to one of the following three lycosoid taxa: the family Lycosidae, the family Trechaleidae, or the subfamily Rhoicininae (with *Shinobius* considered a member of the latter taxon, Yaginuma 1991; Sierwald 1993). The familial placement of Rhoicininae is uncertain (Sierwald 1993; Carico 1993), but its members are currently listed in Trechaleidae (see Platnick 2002). The exceptions referred to include other lycosoids (sensu Griswold et al. 1999) (e.g., the ctenid *Cupiennius*, Barth et al. 1991; Silva Davila in press) as well as non-lycosoids (e.g., the nesticids *Nesticus*, *Eidmannella*, Nielsen 1932:201; Bristowe 1958:223; Pötzsch 1963:30; the zorids *Voraptus*, *Neoctenus*, Lawrence 1964:34; Silva Davila in press, though in the latter paper *Neoctenus* is transferred to Trechaleidae). The spinnerets are also involved in carrying the egg sac in at least some genera within the lycosoid family Pisauridae (see Discussion), but here the chelicerae play the principal role in securing the egg sac, which is positioned below the sternum. At times, lycosids hold the egg sac in a similar attitude; e.g., during the last phase of egg sac construction, when assisting in spiderling emergence, or sometimes when fleeing, after one has attempted to take the egg sac away from the mother (e.g., Montgomery 1903; Lécaillon 1905). And, conversely, some pisaurids occasionally "drag the sac from the spinnerets alone in the same manner as a lycosid" (Bishop 1924:28).

As described in Carico (1993), Sierwald (1990a, 1993), Scheffer (1905) and literature cited by the first two authors, differences exist among lycosids, trechaleids, rhoicinines, and pisaurids with regard to egg sac structure and the maternal care afforded post-emergent spiderlings. Typically, the egg sacs of lycosids and rhoicinines are spherical or lenticular, those of pisaurids are spherical, while those of trechaleids are hemispherical. A seam joining the upper and lower valves of the egg sac is apparent among lycosids, trechaleids, and some rhoicinines (*Shinobius*), but not in some

other rhoicinines (*Rhoicinus*) or pisaurids, and only in trechaleids is a 'skirt' (Carico 1993) produced at the seam.

Lycosid, trechaleid, and rhoicinine females continue to carry their progeny for a number of days after they have emerged from the egg sac (lycosids about 2–14 days, e.g., McCook 1884; Montgomery 1903:72,76,82,90; Engelhardt 1964:303,387; *Trechalea* about 17–19 days, Carico et al. 1985; *Shinobius* about 4 days, Kaihotsu 1988). But while lycosid spiderlings climb onto the mother's abdomen during this period, trechaleid spiderlings and at least *Shinobius* spiderlings (among rhoicinines) climb onto the outside of the egg sac, which the female continues to carry. However, Yaginuma (1991), specifying two *Arctosa* and one *Hygrolycosa* species, reports that transport on the egg sac, rather than on the mother's abdomen, also occurs in some lycosids. In those instances in which trechaleid spiderlings have been observed on the mother's abdomen, this appears to be due to crowding on the egg sac with consequent spill-over (Carico 1993), just as lycosid spiderlings may spill over onto their mother's cephalothorax.

Among pisaurids (where known), the egg sac is carried by the female until shortly before the young emerge, or at latest when the first spiderlings begin to emerge (Gertsch 1979:197). Typically, the egg sac is then secured within a nursery web. The mother builds the network of silk fibers that constitute the nursery web before and/or after the end of the egg-sac-carrying period, often on vegetation, with the spiderlings adding fibers after their emergence. The post-emergent spiderlings remain within the nursery web, guarded by the mother (though see Montgomery 1909: 556; Forster 1967:84), for a period of time that again varies considerably, sometimes even within a species (e.g., *Dolomedes fimbriatus* (Clerck 1757) spiderlings may remain in the nursery web from 3 or 4 days (Bristowe 1958:191) to about 3 weeks (Nielsen 1932: 134)). After this period the spiderlings disperse. Kaihotsu (1988) reports that *Shinobius* females, after carrying their young on the outside of the egg sac for a few days, then hang the egg sac with spiderlings in a nursery web, where the spiderlings remain for about one day.

This study is concerned with the specific silk glands used by lycosids for attaching the egg sac to the spinnerets. The impetus for the study can be explained as follows. Observations made on spinnerets by a number of workers indicated that a certain category of ampullate silk glands, what we call secondary (2°) ampullate silk glands, are functional in juvenile spiders of most, if not all, entelegyne taxa. However, in only some entelegynes are 2° ampullate glands also functional in adults (sometimes only in the females, as in lycosids). The only role assigned to these silk glands that we were aware of when we began this study is to produce silk fibers during one specific period in the molt-intermolt cycle of juveniles (detailed below). The question thus arose, what are 2° ampullate silk glands used for when they are retained in adults? It occurred to us that if these silk glands are involved in egg sac attachment in lycosoids, it might be a situation in which we could, in effect, catch spiders in the act of drawing fibers from these glands and, thus, demonstrate their use in at least one specific application in certain adult spiders. At that time we were not aware that Carico (1993) had already observed certain 2° ampullate gland fibers being used for egg sac attachment to the spinnerets in trechaleids. As we describe below, trechaleids and the lycosids that we have examined (primarily *Pardosa*) show similarities and differences with respect to egg sac attachment, including in their use of 2° ampullate silks. In partial answer to the above question, all we know at this time is that adult females of at least some lycosid and trechaleid (Carico 1993) genera use silk from 2° ampullate glands to help secure the egg sac to the spinnerets.

To provide a better overall perspective on 2° ampullate silk glands and their roles, the following section reviews different categories of ampullate silk glands. It is followed by four sections dealing with nubbins and tartipores, protuberances present in some spinning fields. These sections are included because our interpretations of spinneret micrographs obtained during this study rely on and make reference to these protuberances. And because our basis for distinguishing nubbins from tartipores differs from that of earlier authors, and also differs from our own earlier views, the first of these four sections explains how we arrived at our current definitions for nubbins and tartipores. The last three sections review

some aspects of the occurrence of these protuberances. We hope this overview will be useful in light of the growing importance of these structures in phylogenetic studies. In addition to presenting observations made on the spinnerets and egg sacs of some female lycosids, this paper contains comparative observations made on the spinnerets of male lycosids and the spinnerets of spiders from several other families in which adult females retain apparently functional 2° ampullate glands.

Categories of ampullate silk glands and their roles.—The ampullate silk glands of spiders within the Orbiculariae and some other taxa (e.g., Hersiliidae, Kovoor 1984; Segestriidae, Clubionidae, Gnaphosidae, Thomisidae, Kovoor 1987; Oxyopidae, Kovoor & Muñoz-Cuevas 1998) can be divided, on the basis of histochemical differences, into major ampullate silk (MaA) glands and minor ampullate silk (MiA) glands (reviewed in Kovoor 1977, 1987; also Kovoor & Peters 1988). The ducts of the MaA glands connect to spigots located on the anterior lateral spinnerets (ALS) while MiA gland ducts connect to spigots on the posterior median spinnerets (PMS). In some other spiders, however, including the Lycosidae, histochemical differences are not readily apparent between those ampullate glands with ducts that empty on the ALS versus those with ducts emptying on the PMS (Kovoor 1976, 1987). One may therefore question the validity of recognizing two different types of ampullate glands in such taxa. Nevertheless, for clarity and in keeping with precedents (e.g., Platnick et al. 1991:2), any ampullate glands with ducts attached to the ALS will be called MaA glands and any with ducts attached to the PMS will be called MiA glands (Table 1).

In more basal araneoids, including those in the families Araneidae and Tetragnathidae (Griswold et al. 1998), both the MaA and MiA glands can be further subdivided into a single pair of primary (1°) MaA/MiA glands and two pairs of 2° MaA/MiA glands (Table 1) (Townley et al. 1993; Tillinghast & Townley 1994). Observations made on spinnerets (Coddington 1989; Forster et al. 1990; Peters & Kovoor 1991; Hormiga 1994a,b, 2000; Griswold et al. 1998) suggest a tendency for the more derived araneoids to lack 2° MiA glands. The 1° MaA and 1° MiA glands function in each juvenile stadium from immediately after ecdysis (even as the spider is hanging by its 'molting threads') until about the beginning of the following proecdysis (the few days preceding ecdysis during which internal changes take place in preparation for ecdysis), as well as throughout adulthood (Townley et al. 1993). During proecdysis these glands are remodeled, rendering them temporarily nonfunctional (Townley et al. 1991). The task of producing ampullate silk during each proecdysis is taken over by one of the two pairs of 2° MaA glands and one of the two pairs of 2° MiA glands. Each pair of 2° ampullate glands cycles through growth and regression phases, reaching maximum size and accumulation of luminal contents at proecdyses in every other juvenile stadium, with one pair of 2° MaA/2° MiA glands producing silk during proecdysis in even-numbered stadia and the other pair functioning in odd-numbered stadia (Townley et al. 1993). Because only one of the two pairs of 2° MaA/2° MiA glands produces silk in a given juvenile stadium (i.e., is 'open', see Table 1), there is only one 2° MaA spigot on each ALS and one 2° MiA spigot on each PMS of juveniles (in addition to the single 1° MaA spigot and single 1° MiA spigot on each ALS and PMS, respectively). After the final molt, with no additional proecdyses to pass through, both pairs of 2° MaA/2° MiA glands degenerate (Sekiguchi 1955b; Townley et al. 1991). Thus, 2° ampullate glands do not function in adults and only nonfunctional vestiges, termed nubbins (Coddington 1989; Yu & Coddington 1990), of 2° ampullate spigots are present on adult ALS and PMS (Sekiguchi 1955b; Peters 1955; Mikulska 1966; Wilson 1969). This situation exists in both sexes. External examinations of spinnerets indicate that this description, outlined in Table 1, applies not only to basal araneoids, but to some non-araneoids (e.g., oxyopids, Kovoor & Muñoz-Cuevas 1998), and, whatever their superfamilial placement, to some mimetids (see data for *Mimetus* in Table 3; see also mimetid spinneret micrographs in Platnick & Shadab 1993). Interestingly, it may be that the above description applies to some species within the mimetid genus *Ero*, but not others (cf. figs. 29, 30 with figs. 41, 42 in Platnick & Shadab 1993, noting especially the presence of a MiA nubbin and MiA tartipore (tartipore defined below) in fig. 42 and the

Table 1.—The division of ampullate silk glands into different categories on the basis of which spinnerets receive their ducts (major vs. minor), whether glands are functional in both juveniles and adults or just in juveniles during proecdysis (primary (1°) vs. secondary (2°)), and whether 2° ampullate glands have an outlet to the extracorporeal environment in a given stadium or not (open vs. blocked). This scheme is based on observations made primarily on *Araneus* (Townley et al. 1993; Townley 1993; Tillinghast & Townley 1994) and applies to both sexes. Lycosids and the species from the other families in Table 2 deviate from this table only in that 2° MaA and 2° MiA glands of females apparently function not only in juveniles during proecdysis, but one pair of each is functional in adults as well. The double-headed arrows between open and blocked 2° ampullate glands indicate that a given pair of glands is alternately open and blocked; open throughout one stadium (i.e., from one ecdysis to the next), blocked throughout the following stadium, open again in the stadium after that, and so on.

Ampullate Silk Glands
6 pairs
produce silk fibers used in a variety of applications including draglines and non-sticky structural elements of webs

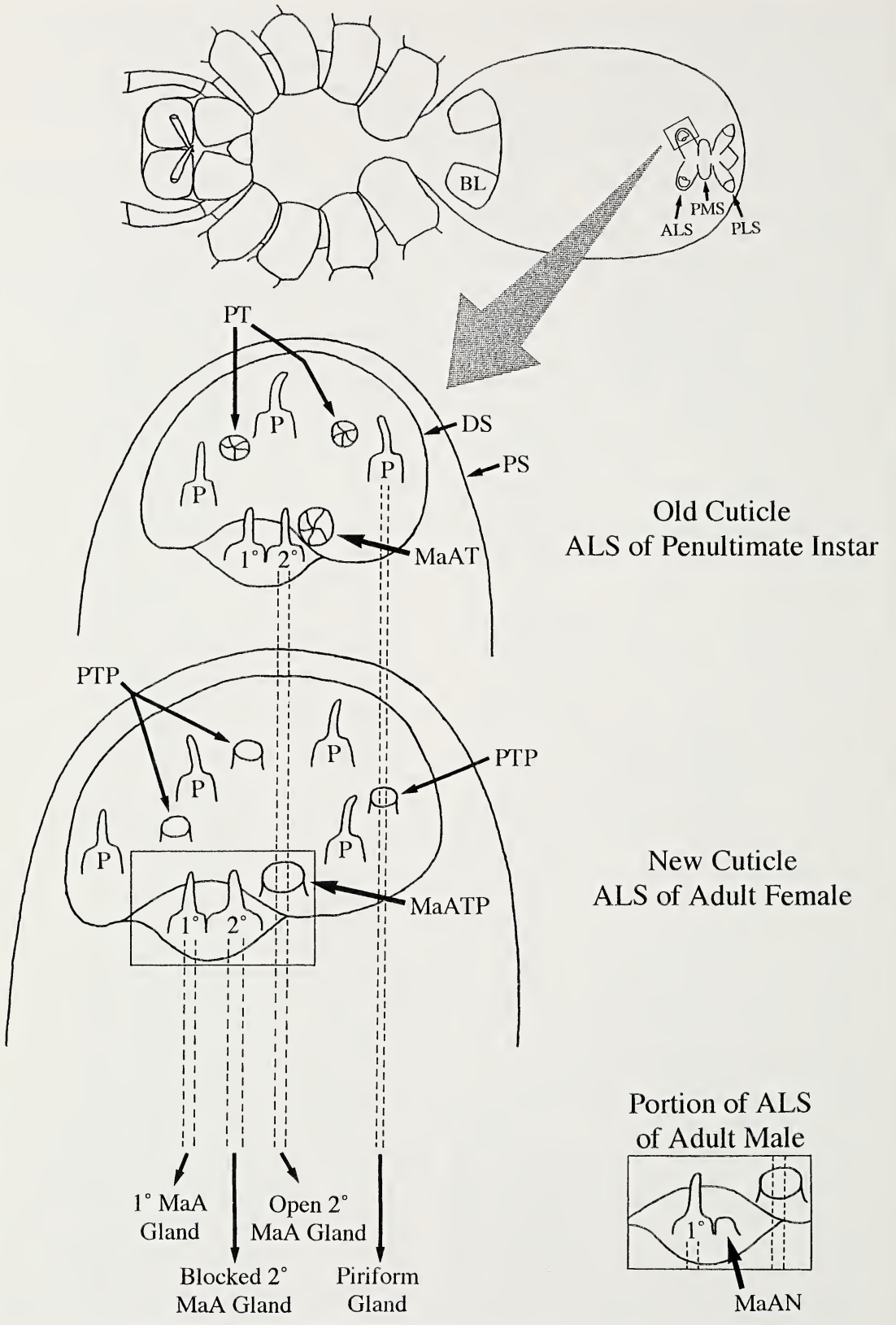
Major Ampullate Silk (MaA) Glands 3 pairs ducts lead to anterior lateral spinnerets (ALS)		**Minor Ampullate Silk (MiA) Glands** 3 pairs ducts lead to posterior median spinnerets (PMS)	
1° MaA Glands 1 pair functional in juveniles (from ecdysis to start of next proecdysis) and adults	**2° MaA Glands** 2 pairs functional in juveniles only (during proecdysis only)	**1° MiA Glands** 1 pair functional in juveniles (from ecdysis to start of next proecdysis) and adults	**2° MiA Glands** 2 pairs functional in juveniles only (during proecdysis only)
	Open 2° MaA Glands ⟷ **Blocked 2° MaA Glands** 1 pair ducts connect to spigots that open to the outside environment ⟷ ducts do not connect to spigots that open to the outside environment		**Open 2° MiA Glands** ⟷ **Blocked 2° MiA Glands** 1 pair ducts connect to spigots that open to the outside environment ⟷ ducts do not connect to spigots that open to the outside environment

absence of these protuberances in fig. 30; see also Schütt 2000:145).

In contrast to the situation just described for basal araneoid taxa, examinations of spinnerets from spiders in certain amaurobioid (sensu Griswold et al. 1999) and dionychan (sensu Coddington & Levi 1991) families, including the Lycosidae (Table 2), reveal a sexual dimorphism wherein males appear to conform to the above description, but females do not (Fig. 1). Instead, adult females retain apparently functional 2° MaA and 2° MiA spigots, one pair of each, indicating that they use 2°, as well as 1°, ampullate glands as adults. In trechaleids, Carico (1993) has observed the use of 1° and 2° MiA silks by adult females for securing the egg sac to the spinnerets. Here we report that adult female *Pardosa* use 1° and 2° MaA and 1° and 2° MiA silks to attach their egg sacs to their spinnerets. The 2° ampullate fibers have greater diameters than the 1° ampullate fibers, indicating a greater contribution from the 2° ampullate glands to the support of the egg sac.

Terminology.—*Nubbins and tartipores:* As mentioned, the term 'nubbin' has been applied to cuticular protuberances on adult ALS and PMS that appear to be nonfunctional vestiges of 2° MaA and 2° MiA spigots, respectively. Other cuticular protuberances, scattered within piriform and aciniform spinning fields (Kovoor 1986; Platnick 1990; Yu & Coddington 1990), as well as on the PMS and posterior lateral spinnerets (PLS) of at least some mygalomorphs (Glatz 1973; Palmer 1990), have been called 'tartipores' (Shear et al. 1989; Yu & Coddington 1990). Originally, the distinction between a nubbin and a tartipore was based on whether the protuberance is a morphological singular and can, therefore, be uniquely designated (nubbin) or if it is one of several, or many, such structures on a single spinneret that are designated collectively (tartipore) (Yu & Coddington 1990; see also Coddington 1989:81). Both nubbins and tartipores were tentatively interpreted to be vestigial spigots. Additional observations, however, revealed that the protuberances identified as tartipores are not vestigial spigots. Instead, they are the remains of collared openings that formed in the cuticle when it was first being laid down during proecdysis beneath the old cuticle (Townley et al. 1993). The openings allowed silk gland ducts to maintain their attachments to spigots on the old cuticle during proecdysis, despite the formation of the intervening new cuticle (Fig. 1). Thus, while some protuberances do seem to be vestigial spigots, others have a very different origin, being remnants of these openings.

After realizing that we were actually dealing with two different categories of cuticular protuberances, we made an ill-devised attempt to both retain the original distinction between nubbins and tartipores (singulars versus multiples) and distinguish vestigial spigots from remnants of openings by use of the adjectives 'vestigial-type' and 'non-vestigial-type', respectively (Townley et al. 1993). We soon abandoned this approach in favor of another, not previously published, that is concerned only with the two different origins of the protuberances under consideration (for further explanation see Townley 1993:7, 8). The latter approach, which we will follow in this paper, retains the terms nubbin and tartipore, but defined as follows: *Nubbin:* a nonfunctional, only partially formed, i.e. vestigial, spigot, either morphologically singular or multiple. *Tartipore:* a cuticular scar, morphologically singular or multiple, that results, after ecdysis, from a collared opening forming in the developing exoskeleton during proecdysis; the opening accommodates a silk gland duct, allowing the duct to remain attached to a spigot on the old exoskeleton during proecdysis. By these definitions the protuberances that were initially called tartipores (those among piriform and aciniform spigots) are still called tartipores (Fig. 1). However, only some of the structures previously referred to as nubbins are still called nubbins by our definition. For example, as in earlier reports, we identify as nubbins those nonfunctional protuberances in some adults that occur where functional 2° MaA/2° MiA spigots would have formed if the spider had instead molted to yet another juvenile instar (see Figs. 1, 13, 15). But there are other protuberances near ampullate spigots in many adult and juvenile araneomorphs, previously called nubbins (e.g., Yu & Coddington 1990; Townley et al. 1991, 1993; Tillinghast & Townley 1994), that we now identify as ampullate tartipores, including the "second nubbin" on the PMS of adult anapids and some synotaxids (Griswold et al. 1998:41) and the "second remnant" on the PMS of adult oxyopids (Kovoor & Muñoz-Cuevas 1998:


BL
PMS
ALS
PLS
PT
P
DS
PS
MaAT
1°
2°
Old Cuticle
ALS of Penultimate Instar
PTP
MaATP
New Cuticle
ALS of Adult Female
1° MaA Gland
Open 2° MaA Gland
Blocked 2° MaA Gland
Piriform Gland
Portion of ALS of Adult Male
MaAN

136). This is not the first time such protuberances have been referred to as tartipores (Platnick & Forster 1993:7, 9; Griswold et al. 1998:11), but in these earlier instances the distinction made between tartipores and nubbins was not stated. The term tartipore was perhaps applied solely because of the resemblance between ampullate tartipores and the more well known tartipores in piriform and aciniform spinning fields, rather than because of recognition of what tartipores, as here defined, represent. As indicated above, ampullate tartipores mark the sites where 2° ampullate gland ducts passed through the cuticle during the most recent proecdysis, enabling 2° ampullate glands to function throughout proecdysis (Fig. 1). Note that Fig. 1 depicts only the ALS from a lycosid and so only spigots, tartipores, and ducts of MaA and piriform glands are shown. Bear in mind that a comparable situation exists on the PMS with the spinning apparatus of MiA and aciniform glands, respectively.

Ampullate gland nubbins versus ampullate gland tartipores.—When examining spinnerets, care must be taken if one wishes to determine whether ampullate nubbins and tartipores are present or not, as well as distinguish the former category from the latter. Viewing the spinnerets at various angles and from different directions is sometimes required. In some adult araneoids, for example, the MiA nubbin and MiA tartipore on a PMS often occur side by side (e.g., Coddington 1989:fig 16; Platnick et al. 1991:fig. 271, lower black arrow, tartipore on left, nubbin right; Townley et al. 1991:fig. 24; lower arrow to tartipore, upper to nubbin; Hormiga et al. 1995:fig. 16C, nubbin left, tartipore right) and can be interpreted as a single structure if viewed at too low a magnification or from an

←

Figure 1.—Schematic diagram of the left anterior lateral spinneret (ALS) of a female lycosid during proecdysis, shortly before the ecdysis that yields an adult. The upper ALS diagram represents the cuticle of the penultimate instar which will be cast off at ecdysis. The ALS diagram below this represents the underlying, newly-formed cuticle which will be part of the exoskeleton of the adult. Shown is the entire distal segment (DS) of the ALS, to which the major ampullate (MaA) spigots (labeled as '1°' and '2°') and piriform spigots (P) are restricted, atop the more distal portion of the ALS proximal segment (PS).To aid orientation, a much less magnified depiction of the same part of the left ALS is enclosed by a box in the ventral view of the spider, shown at top, in which the spinnerets are presented as if artificially spread. By late proecdysis, the duct of the primary (1°) MaA gland, previously connected to a spigot on the old cuticle (that labeled '1°'), has just been re-modeled (Townley et al. 1991, 1993) and is now connected to a spigot on the new cuticle (again labeled '1°') (silk gland ducts are indicated by dashed lines). Thus, the 1° MaA gland, nonfunctional during proecdysis, will again be functional immediately after ecdysis. Collared openings (tartipore progenitors) form in the new cuticle to accommodate the ducts of any silk glands that are to remain functional throughout proecdysis. The ducts of two such silk glands are shown connected to spigots on the old cuticle. After ecdysis the collapsed forms of these openings (tartipores) will remain evident in the new cuticle. A single MaA tartipore progenitor (MaATP) forms on each ALS of the new cuticle to accommodate the duct of a secondary (2°) MaA gland. Multiple piriform tartipore progenitors (PTP) also form on each ALS, one per piriform gland duct. (For clarity only a few piriform spigots are shown, and of those on the old cuticle, the duct connected to only one is shown. In reality, more piriform spigots are present and it appears that each piriform spigot on the old cuticle remains connected to a functioning duct, thus requiring the formation of one PTP on the new cuticle for each piriform spigot on the old cuticle.) The 2° MaA gland identified as 'open' will become 'blocked' at ecdysis (because its outlet, the spigot, will be lost along with the rest of the old cuticle), and, conversely, that identified as 'blocked' will become 'open' (since the 2° MaA spigot it is connected to will be open to the outside environment after ecdysis). The portion of the female new cuticle shown within a box differs from the situation in males (depicted at lower right) because 2° ampullate spigots do not form in adult males. Only ampullate nubbins (MaA nubbin (MaAN) on ALS, MiA nubbin on PMS) form in the positions occupied by 2° ampullate spigots in adult females and, thus, all 2° ampullate glands are 'blocked' and nonfunctional in adult males. Structures not drawn precisely to scale. BL, book lung; ALS, anterior lateral spinneret; PMS, posterior median spinneret; PLS, posterior lateral spinneret; DS, distal segment of anterior lateral spinneret; PS, proximal segment of anterior lateral spinneret; P, piriform gland spigot; PT, piriform tartipore; PTP, piriform tartipore progenitor; 1°, primary major ampullate gland spigot; 2°, secondary major ampullate gland spigot; MaAT, major ampullate tartipore; MaATP, major ampullate tartipore progenitor; MaAN, major ampullate nubbin.

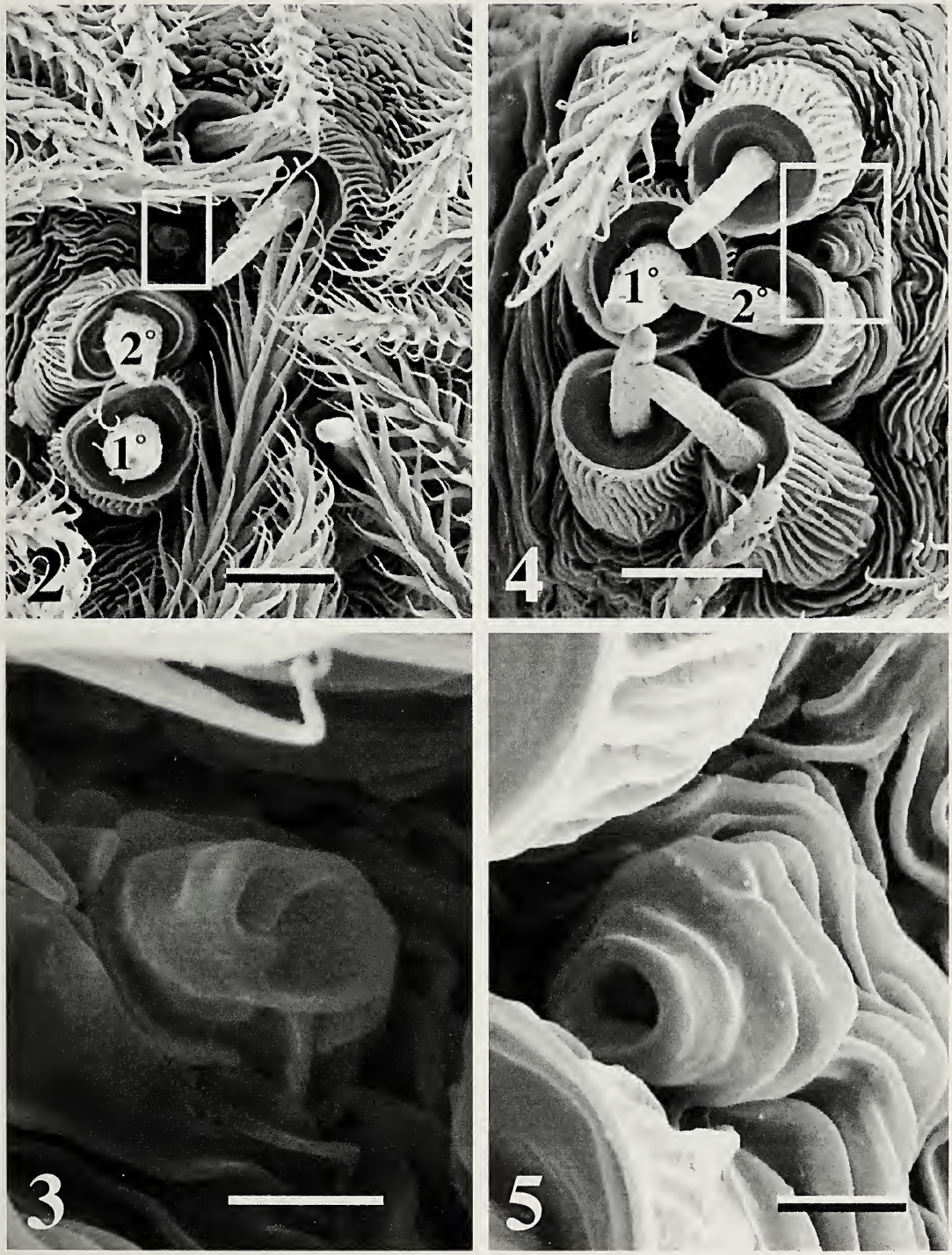
inopportune angle, or if the MiA nubbin is especially small. In describing the PMS of adult males of two anapid species, Platnick et al. (1991:60) noted the presence of "a large posterior minor ampullate gland spigot accompanied by a vestigial remnant bearing a short lobe on its medial side". The "vestigial remnant" is a MiA tartipore, the "short lobe" is a MiA nubbin. Even with careful observation it can sometimes be difficult, especially with certain species, to discern a given tartipore or nubbin. We were puzzled for a time by our inability to spot a MaA tartipore on the ALS of juvenile and adult *Araneus cavaticus* (Keyserling 1882) until it became clear that this tartipore occurs at a site where, in this species, the cuticle is typically compressed or overhung by the piriform spinning field and the tartipore is obscured (Townley et al. 1993). In contrast, single or multiple MaA tartipores are often clearly visible in many other araneomorphs as a number of published micrographs attest (several were cited in Townley et al. 1993:36 as "non-vestigial-type MaA nubbins"; other examples include Platnick et al. 1991: fig. 16, multiples in *Gradungula*, fig. 39, a single in *Thaida*, fig. 277, a round single in *Pachygnatha* next to smaller oblong MaA nubbin; Harvey 1995: fig. 11, a single in *Ambicodamus* posterolateral to the 2° MaA spigot; Davies 1998a:fig. 68, a single in *Jalkaburra* lateral to the 2° MaA spigot; Platnick 1999: fig. 3, a single in *Liocranoides* between and lateral to 1° and 2° MaA spigots; Hormiga 2000:plate 42B, a single in *Laminacauda* posterolateral to MaA nubbin, larger than the multiple piriform tartipores). In this paper, single MaA tartipores can be seen in Figs. 1, 8, 9, 12, 13, 16, 18, 22, 24, 26, 28, 30, 32, 34, 36, 40 & 41 and single MiA tartipores can be seen in Figs. 10, 11, 14, 15, 19–21, 23, 25, 27, 29, 31, 33, 35, 37–39 & 42.

Given that the occurrence and number of ampullate "nubbins" (i.e., ampullate nubbins and/or tartipores) are being used as characters in cladistic analyses (Coddington 1990; Hormiga et al. 1995; Scharff & Coddington 1997; Griswold et al. 1998, 1999; Hormiga 2000), accurately determining the presence/absence of ampullate tartipores and nubbins, and making a clear distinction between the two, can only aid phylogenetic studies.

Occurrence of tartipores.—Tartipores can occur in the exoskeletons of adults and juveniles, at least as early as second instars (see Methods for the definition of the first instar used in this paper). We have not seen and are not aware of any reports of tartipores in first instars. However, given the occurrence of functioning silk glands and spigots in postembryos of at least some mygalomorph taxa (Bond 1994), the possibility of tartipores in first instars of such taxa cannot be dismissed. But at least for those araneomorphs in which functional silk glands and spigots first appear in first instars, tartipores do not need to form until deposition of the second instar cuticle begins. Consequently, for such spiders, tartipores would first be seen in second instars. (The presence of one, presumably 1°, MaA spigot base per ALS in *Nephila* (Tetragnathidae) postembryos has been described by Bleher (2000), but their ability to produce silk is uncertain and only the ducts of 2° ampullate glands are known to be accommodated by ampullate tartipores.)

It is of interest, therefore, that protuberances, reminiscent of but recognizably different from tartipores, are sometimes evident on the ALS and PMS of first instars, in positions consistent with those of ampullate tartipores in later instars. We have seen them near 2° ampullate spigots on the ALS and PMS of first instar *Pardosa xerampelina* (Keyserling 1877) (Figs. 2–5) and *Octonoba sinensis* (Simon 1880) (Uloboridae), and on the PMS of first instar *Argiope aurantia* Lucas 1833 (Araneidae) and *Herpyllus ecclesiasticus* Hentz 1832 (Gnaphosidae). We tentatively refer to them as 'pre-tartipores' (not to be confused with the tartipore progenitors referred to in Fig. 1). If they truly are precursors of the tartipores in later instars, their occurrence suggests that the epithelial cells that are capable of forming tartipores, at least ampullate tartipores, are already determined by the postembryo stage.

Occurrence of nubbins.—In general, nubbins as here defined occur in adults, being more abundant in males (largely since silk glands used solely or primarily in prey capture tend to regress in adult males), and are ontogenetically vestigial. That is, they are located in adults in positions where functional spigots would have formed if the spider had remained a juvenile after its most recent molt. In addition to the MaA and MiA nubbins present in a variety of adult male and female araneocla-



Figures 2–5.—ALS and PMS from a first instar *Pardosa xerampelina* (removed from dorsum of its mother's abdomen) showing protuberances, tentatively termed 'pre-tartipores', in positions that are held by ampullate tartipores in later instars: 2. Right ALS, entire spinning field shown (two MaA and three piriform spigots), pre-tartipore in box; 3. Higher magnification of pre-tartipore from Fig. 2; 4. Right PMS, entire spinning field shown (two MiA and three aciniform spigots), pre-tartipore in box; 5. Higher magnification of pre-tartipore from Fig. 4. Posterior at top, lateral at right in all four figures. Scale bars (2, 4) = 5 μm; (3, 5) = 1 μm.

Table 2.—Spider species in which adult females are known to have two MaA spigots (1° and 2°) on each ALS and two MiA spigots (1° and 2°) on each PMS while adult males have one MaA spigot (1°) on each ALS and one MiA spigot (1°) on each PMS. The families listed here are almost certainly not the only ones that contain species fitting this description. Note that *Neoramia* (Agelenidae) apparently do not fit this description (Griswold et al. 1999); nor do some salticid genera (see 'Ampullate gland spigot, nubbin, tartipore complements' in Results) or several amaurobiid genera, including *Amaurobius* (see 'Comparative ampullate gland spigot morphology' in Discussion). Also, this description may not extend to all *Coras* species (see 'Ampullate gland spigot, nubbin, tartipore complements' in Results).

Family	Species	References
Lycosidae	*Gladicosa gulosa* (Walckenaer 1837)	this study
	Pardosa amentata (Clerck 1757)	Richter 1970
	Pardosa lapidicina Emerton 1885	this study
	Pardosa lugubris (Walckenaer 1802)	Wąsowska 1977
	Pardosa modica (Blackwall 1846)	this study
	Pardosa moesta Banks 1892	this study
	Pardosa saxatilis (Hentz 1844)	this study
Pisauridae	*Dolomedes scriptus* Hentz 1845	this study
	Pisaurina mira (Walckenaer 1837)	this study
Agelenidae	*Agelena labyrinthica* (Clerck 1757)	Kokociński 1968
	Agelenopsis naevia (Walckenaer 1842)	this study
	Agelenopsis potteri (Blackwall 1846)	this study
Amaurobiidae	*Coras aerialis* Muma 1946	this study
Thomisidae	*Misumenops asperatus* (Hentz 1847)	this study
	Xysticus cristatus (Clerck 1757)	Wąsowska 1977
Philodromidae	*Tibellus oblongus* (Walckenaer 1802)	Wąsowska 1967, 1977; this study
Clubionidae	*Clubiona phragmitis* C.L. Koch 1843	Mikulska 1969; Wąsowska 1969; Wiśniewski 1986a,b
Miturgidae	*Cheiracanthium mildei* L. Koch 1864	this study
Salticidae	*Salticus scenicus* (Clerck 1757)	this study

dans, flagelliform and aggregate nubbins form on the PLS of many adult male araneoids (Sekiguchi 1955a; Peters & Kovoor 1991:fig. 3b; Platnick et al. 1991:fig. 275; Townley et al. 1991:fig. 16; Townley 1993:fig. 16; Griswold et al. 1998:figs. 25D, 39D, 43D), though a number of males within the 'reduced piriform clade' of Griswold et al. (1998) (see also Hormiga 2000) and the Micropholcommatidae (Schütt 2000) retain the aggregate/flagelliform spigot triad. Other examples include aciniform nubbins on the PMS (Müller & Westheide 1993) and PLS (pers. obs.) of adult male *Argiope* and on the PMS of some adult male uloborids (Kovoor & Peters 1988:53), pseudoflagelliform nubbins on the PLS and paracribellar nubbins on the PMS of some adult male deinopoids (Kovoor & Peters 1988; Peters 1992), paracribellar nubbins on the PMS of adult male austrochilids (Peters 1983; Platnick et al. 1991:fig. 33), and nubbins of uncertain gland type on the ALS of adult male *Hypochilus*, next to the single, large ampullate spigot (Platnick et al. 1991:fig. 4; Townley 1993:figs. 17D,E). By the interpretation of Platnick et al. (1991:51) the latter would be MaA nubbins.

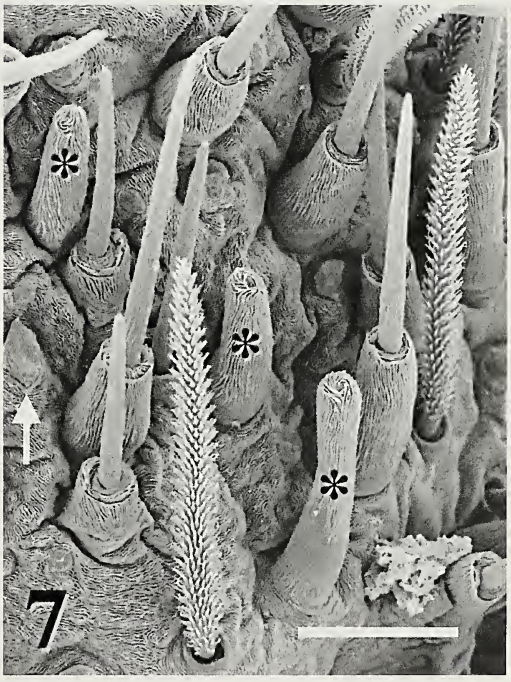
Among the examples of exceptions to the general rule are nubbins occasionally seen in early instar *Cyrtophora* (Araneidae) that suggest phylogenetic vestiges of either aggregate or flagelliform spigots. In an examination of six first instar *Cyrtophora citricola* (Forskål 1775), on one PLS Peters (1993:figs. 11b, c) observed a single "shaft-like structure" on the vestigial plate of the aggregate-flagelliform triad. (On nine PLS one or two "knobs with pores" were seen on these vestigial plates, but we do not interpret these as nubbins.) Nubbins that are also apparently phylogenetic vestiges of aggregate spigots are often retained right up to maturity in female *Drapetisca socialis* (Sundevall 1833) (Linyphiidae); functional aggregate spigots are absent throughout the ontogeny of these spiders (Schütt 1995). The occurrence of a MaA nubbin on the ALS of penultimate instar female *Malala lubinae* Da-

vies 1993 (tentatively Amaurobiidae, Platnick 2002) (Davies 1993) is also atypical.

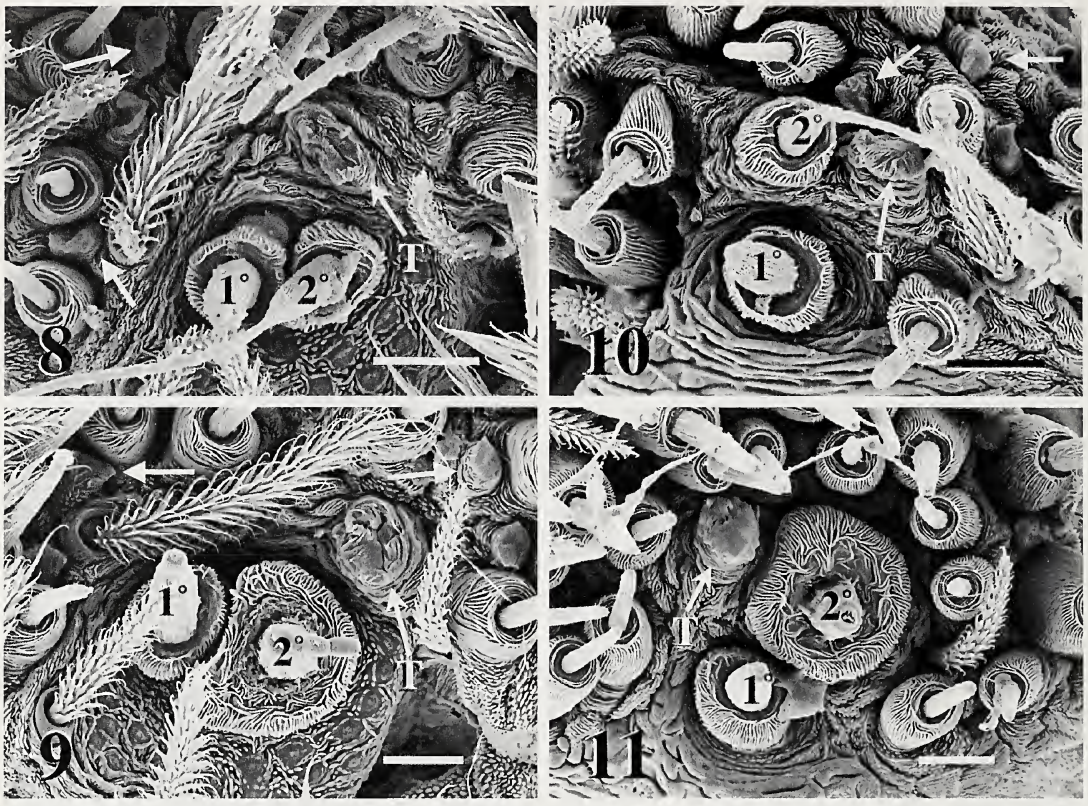
In the course of the present study we observed a few consistently-located aciniform nubbins on the PMS (Figs. 19–21) and PLS (Figs. 6, 7) of some juvenile and adult lycosids, the details of which are given in the Results. The reason these nubbins form with as much regularity as we have seen, particularly in *Hogna*, remains to be explained. Certainly, it is not unusual in an aciniform or piriform spinning field to encounter occasional incompletely formed spigots (i.e., nubbins). But such nubbins are presumably teratological, given their random and, typically, asymmetrical occurrence (present on one spinneret but not its pair). The occurrence of aciniform nubbins in *Hogna*, on the other hand, is neither random nor asymmetrical. Because they are present in juvenile females, they are another example of atypical nubbins.

Nubbins resulting from different gland types and, in some cases, nubbins of the same gland type in different taxa vary considerably in the extent to which their development proceeds before it is aborted. Thus, nubbins may range from being small mounds or small spherical or oblong protuberances, e.g., in the case of some MaA and MiA nubbins, to being essentially normal spigot bases on which shafts never develop, e.g., in the case of many aciniform and paracribellar nubbins of adult males, as well as the aforementioned nubbins of adult male *Hypochilus*. It may even be with these more developed nubbins that a shaft does sometimes form on the spigot base, but the junction of the base and shaft appears malformed, suggesting that the spigot and/or the silk gland it serves actually are not functional.

At the opposite extreme, we have indications that in some taxa (the three examples seen thus far are dionychans) it is common for certain nubbins not to form at all. In an adult male *Salticus scenicus* (Clerck 1757) (Salticidae), we observed single 2° ampullate nubbins on both ALS and the left PMS, but not on the right PMS (Table 3). That this individual had 2° MiA spigots when it was a penultimate instar, on the right PMS as well as the left PMS, is indicated by the MiA nubbin on the left PMS and the MiA tartipores on both PMS. The same situation was seen in an adult male *Tibellus oblongus* (Walckenaer 1802) (Philodromidae) and an adult male *Misumen-*



Figures 6–7.—Right PLS on the last exuvium shed by a female *Hogna* sp. killed while a penultimate instar (i.e. the cuticle of the antepenultimate instar is shown): 6. Three aciniform nubbins, among aciniform (and cylindrical?) spigots, can be seen within the box; 7. Higher magnification of the three aciniform nubbins (*) from Fig. 6, arrow to example of an aciniform tartipore. Posterior at left, lateral at top in both figures. Scale bars (6) = 100 μm; (7) = 25 μm.



Figures 8–11.—Portions of the ALS and PMS containing the ampullate spigots, from an adult female *Pardosa saxatilis* and the last exuvium shed by this individual (i.e. the cuticle of the penultimate instar): 8, 10. Penultimate instar; 9, 11. Adult; 8, 9. Left ALS (posterior at right, lateral at top); 10, 11. Right PMS (posterior at left, lateral at top). Note the relative increase in diameter of the bases of the 2° MaA and 2° MiA spigots in the adult cuticle and that the MiA tartipore and 2° MiA spigot switch positions from one instar to the next. Unlabeled arrows point to examples of piriform (Figs. 8–9) or aciniform (Fig. 10) tartipores. Scale bars = 10 μm.

ops asperatus (Hentz 1847) (Thomisidae), except that for the latter it was on the left PMS that a MiA nubbin was lacking (Table 3). The one MiA nubbin that was present on the *S. scenicus* and *M. asperatus* individuals was very small, as was the right MiA nubbin on a second adult male *M. asperatus*. But the left MiA nubbin on the latter spider was much larger (likewise in the *T. oblongus* individual), clearly showing cuticular sculpturing in the form of longitudinal ridges like those on the bases of the 1° MiA spigots.

Finally, in adult males it is sometimes the case with multiple nubbins that not all of the spigots of a given gland type are represented by nubbins; some appear to develop into functional spigots (at least they have shafts and the base-shaft junctions do not look malformed).

METHODS

Spiders examined.—Spinnerets with attached egg sacs were examined by scanning electron microscopy (SEM) in *Pardosa moesta* Banks 1892 (6 specimens), *Pardosa lapidicina* Emerton 1885 (2 specimens), *Pardosa modica* (Blackwall 1846) (1 specimen), *Pardosa littoralis* Banks 1896 (1 specimen), and *Trochosa ruricola* (De Geer 1778) (1 specimen). The numbers of specimens given include only those that yielded useful information. The *P. littoralis* was collected in central South Carolina. The others were collected in southeastern (se) New Hampshire (NH).

Other spinnerets were also examined, both from several lycosid species (without attached egg sacs) and from species belonging to other families (mostly those in which adult females

retain functional 2° MaA/2° MiA glands) (see Table 3). These were also collected in se NH with the following exceptions: *P. xerampelina* (se NH and southwestern Maine), *Pardosa hortensis* (Thorell 1872) (Luxembourg), *Pardosa lugubris* (Walckenaer 1802) (Luxembourg), *Gladicosa gulosa* (Walckenaer 1837) (southern NH and central Virginia), *Hogna helluo* (Walckenaer 1837) (se NH and central Virginia), *Agelenopsis naevia* (Walckenaer 1842) (central Virginia and western North Carolina), *Coras aerialis* Muma 1946 (se NH and southwestern Maine), *Coras lamellosus* (Keyserling 1887) (southwestern Maine), *Coras montanus* (Emerton 1890) (southwestern NH), *Misumenops oblongus* (Keyserling 1880) (southwestern NH), *Thanatus rubicellus* Mello-Leitão 1929 (central Virginia), and *Phidippus audax* (Hentz 1845) (western Pennsylvania and se NH). Some spiders were collected as juveniles and several antepenultimate or penultimate instar lycosids were prepared for SEM immediately. The others were raised to the adult stage with shed exuvia saved for later examination. Spinnerets on exuvia from a few of the lycosids were prepared for SEM, as described below, in order to compare juvenile and adult spinning fields within the same individual. There were two reasons for examining spinnerets other than lycosid spinnerets to which egg sacs were attached: first, to gain a more complete view of spinning field morphology in lycosids, since attached egg sacs usually make clear viewing of spinning fields difficult or impossible; and, second, to compare spinning fields, especially ampullate spigots, between males and females, between juveniles and adults, and among different lycosid and non-lycosid species.

Spiders were identified using keys and descriptions given, primarily, in Chamberlin & Ivie (1941), Carico (1972, 1973), Dondale & Redner (1978, 1982, 1990), Brady (1979, 1986), Kaston (1981), Roberts (1985), Heimer & Nentwig (1991), Roth (1993), and Prentice (2001). Family assignments and taxonomic citations follow Platnick (2002). Voucher specimens for this study are deposited in the Museum of Comparative Zoology, Harvard University. Most consist only of cephalothoraxes and isolated epigyna since the spinnerets of nearly all collected specimens were processed for SEM.

SEM.—Spinnerets without attached egg sacs were artificially spread in preparation for SEM using the forceps squeeze technique of Coddington (1989), which is a modified version of a technique suggested to that author by J. Kovoor. Carbon dioxide anesthetized spiders were severed at the pedicel, the tines of fine forceps were placed on either side of the spinnerets, one dorsad and one ventrad, and the forceps were squeezed. Any fecal material ejected from the stercoral sac through the anal tubercle was either absorbed with a tissue or rinsed off with distilled water. Inspired by Coddington's (1989) recommendation that live spiders be killed by immersion in boiling water or fixative to spread spinnerets, the spread spinnerets were immersed in boiling water (about 2–5 sec depending on the size of the abdomen) as a kind of first fixation.

The forceps were then held closed using a snug-fitting rubber O-ring (Fine Science Tools, Inc.) and their tips with the held abdomen were inserted through a hole, just large enough to accommodate the forceps, made in the cap of a 20 ml scintillation vial filled with a modified version of Karnovsky's (1965) fixative containing only 1% glutaraldehyde / 1% formaldehyde in 0.1 M cacodylate buffer, pH 7.2. Abdomens were kept refrigerated in the fixative from overnight to several days, allowed to come to room temperature, transferred to distilled water for about 20 min, and then taken through an ethanol series (30%, 50%, 70%, 85%, 95%, 100% used once, 100% fresh; 1–2 hr in each $< 70\%$, 2 hr-overnight in each $\geq 70\%$). Finally, the samples were immersed in hexamethyldisilazane (HMDS) (Nation 1983) overnight and then allowed to air dry. All solutions/solvents were also in scintillation vials so transfers were made by moving cap, forceps, and abdomen as a unit from one vial to the next. Abdomens were mounted on pin-type SEM specimen mounts (stubs) with carbon adhesive tabs (Electron Microscopy Sciences) and carbon paste (Structure Probe, Inc.), sputter-coated with gold/palladium (about 20 nm), and examined on an AMR Model 3300 FE field-emission SEM operated with a 7 kV accelerating voltage.

Some lycosid spinnerets with an attached egg sac were prepared for SEM using the same protocol just described, except that the specimen was not immersed in boiling water and the spinnerets were only partially spread

Table 3.—Ampullate spigot (spig), nubbin (nub), and tartipore (tart) complements in examined spiders belonging to the families listed in Table 2, as well as in examined *Mimetus* (see 'Categories of ampullate silk glands etc.' in the introductory section). Where these complements differed between the left and right spinnerets of an individual, both numbers are shown, with the left spinneret value placed on the left. With the exception of spinnerets from *P. mira* juveniles (identified by P. Sierwald), the spinnerets from those juveniles that are identified to species were obtained either from exuvia shed by spiders raised to adults or from the progeny of identified females. *n* = number of individuals examined. Ad = adult, ALS = anterior lateral spinneret, An = antepenultimate, F = female, M = male, MaA = major ampullate, MiA = minor ampullate, P = penultimate, PMS = posterior median spinneret, U = unknown.

Family Species	Instar	Sex	*n*	Number of MaA spig per ALS	Number of MaA nub per ALS	Number of MaA tart per ALS	Number of MiA spig per PMS	Number of MiA nub per PMS	Number of MiA tart per PMS
Lycosidae									
Gladicosa gulosa (Walckenaer 1837)	Ad	F	4	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Hogna sp.	An	F	1	2	0	1	2	0	1
	P	F	1	2	0	1	2	0	1
Hogna aspersa (Hentz 1844)	Ad	F	1	2	0	1	2	0	1
Hogna helluo (Walckenaer 1837)	P	F	1	2	0	1	2	0	1
	Ad	F	2	2	0	1	2	0	1
Pardosa sp.	An or P	F	6	2	0	1	2	0	1
	P	M	3	2	0	1	2	0	1
Pardosa hortensis (Thorell 1872)	P	F	1	2	0	1	2	0	1
	Ad	F	1	2	0	1	2	0	1
Pardosa lapidicina Emerton 1885	Ad	F	2	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Pardosa littoralis Banks 1896	Ad	F	1	2	0	1	2	0	1
Pardosa lugubris (Walckenaer 1802)	P	M	1	2	0	1	2	0	1
Pardosa modica (Blackwall 1846)	Ad	F	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Pardosa moesta Banks 1892	Ad	F	8	2	0	1	2	0	1
	Ad	M	1	1	1	1	1,2	1,0	1
	Ad	M	1	1	1	1	1	1	1
Pardosa saxatilis (Hentz 1844)	P	F	1	2	0	1	2	0	1
	Ad	F	2	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Pardosa xerampelina (Keyserling 1877)	1st	U	4	2	0	0	2	0	0
	2nd	U	1	2	0	1	2	0	1
	4th	U	1	2	0	1	2	0	1
	Ad	F	1	2	0	1	2	0	1
Trochosa ruricola (De Geer 1778)	3rd	U	1	2	0	1	2	0	1
	Ad	F	1	2	0	1	2	0	1
Trochosa terricola Thorell 1856	Ad	M	1	1	1	1	1	1	1

Table 3.—Continued.

Family Species	Instar	Sex	*n*	Number of MaA spig per ALS	Number of MaA nub per ALS	Number of MaA tart per ALS	Number of MiA spig per PMS	Number of MiA nub per PMS	Number of MiA tart per PMS
Pisauridae									
Dolomedes scriptus Hentz 1845	Ad	F	3	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Dolomedes tenebrosus Hentz 1844	Ad	F	1	2	0	1	2	0	1
Pisaurina mira (Walckenaer 1837)	An or P	F	1	2	0	1	2	0	1
	Ad	F	2	2	0	1	2	0	1
	An	M	1	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Agelenidae									
Agelenopsis naevia (Walckenaer 1842)	Ad	F	2	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Agelenopsis potteri (Blackwall 1846)	Ad	F	6	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Amaurobiidae									
Coras aerialis Muma 1946	Ad	F	1	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Coras lamellosus (Keyserling 1887)	Ad	F	1	2,1	0,1	1	2	0	1
Coras montanus (Emerton 1890)	Ad	M	1	1	1	1	2	0	1
Thomisidae									
Misumena vatia (Clerck 1757)	Ad	F	1	2	0	1	2	0	1
Misumenops asperatus (Hentz 1847)	Ad	F	2	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
	Ad	M	1	1	1	1	1	0,1	1
Misumenops oblongus (Keyserling 1880)	Ad	F	1	2	0	1	2	0	1
Xysticus emertoni Keyserling 1880	3rd	U	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Xysticus ferox (Hentz 1847)	Ad	M	2	1	1	1	1	1	1
Xysticus punctatus Keyserling 1880	4th	U	1	2	0	1	2	0	1
	5th	U	2	2	0	1	2	0	1

Table 3.—Continued.

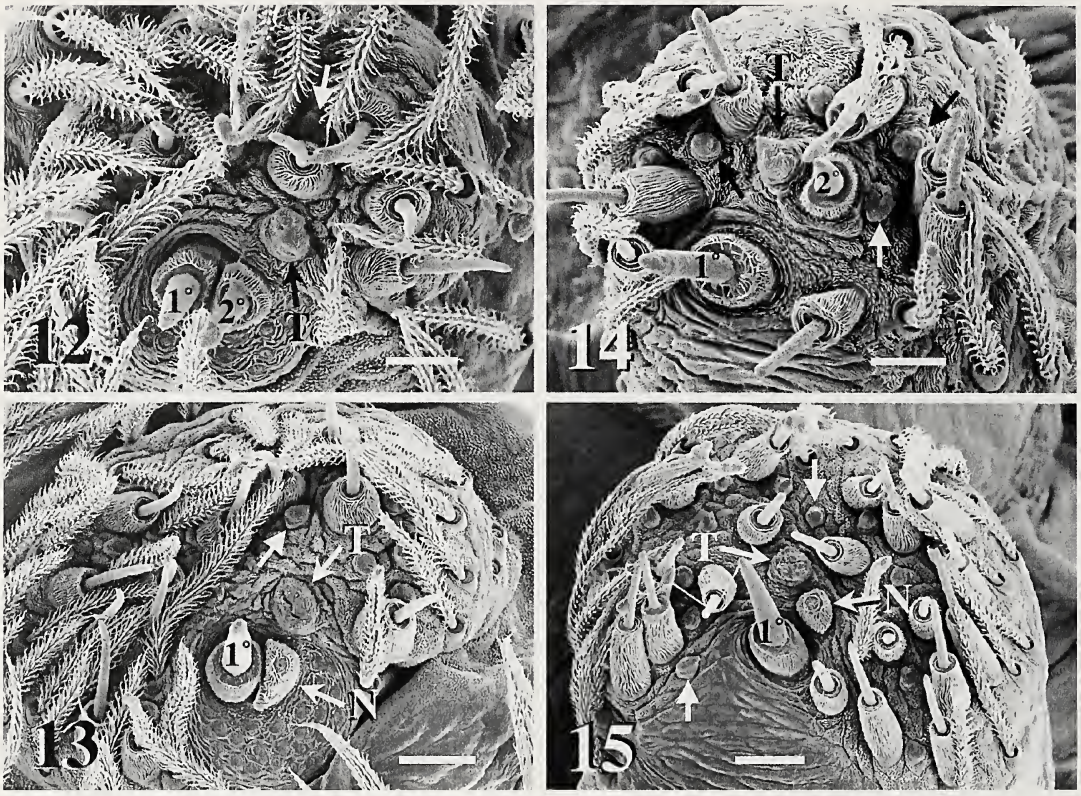
Family Species	Instar	Sex	*n*	Number of MaA spig per ALS	Number of MaA nub per ALS	Number of MaA tart per ALS	Number of MiA spig per PMS	Number of MiA nub per PMS	Number of MiA tart per PMS
Philodromidae									
Philodromus vulgaris (Hentz 1847)	Ad	M	1	1	1	1	1	1	1
Thanatus rubicellus Mello-Leitão 1929	Ad	M	1	1	1	1	1	1	1
Tibellus oblongus (Walckenaer 1802)	Ad	F	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1,0	1
Miturgidae									
Cheiracanthium mildei L. Koch 1864	Ad	F	2	2	0	1	2	0	1
	Ad	M	3	1	1	1	1	1	1
Salticidae									
Phidippus audax (Hentz 1845)	Ad	F	2	2	0	1	2	0	1
	Ad	M	3	2	0	1	2	0	1
Salticus scenicus (Clerck 1757)	Ad	F	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1,0	1
Sitticus pubescens (Fabricius 1775)	Ad	M	1	?	?	?	1	1	1
Mimetidae									
Mimetus notius Chamberlin 1923	Ad	M	2	1	1	1	1	1	1
Mimetus puritanus Chamberlin 1923	Ad	F	2	1	1	1	1	1	1
	Ad	M	2	1	1	1	1	1	1

by placing the forceps more anteriorly on the abdomen with the tines extending only partway across the width of the abdomen. While some spiders were severed at the pedicel, others were left intact. With other specimens, Peters' (1982) paraffin technique was applied after anesthetization, with or without squeezing the abdomen. Hot paraffin was added either dorsally or ventrally to the spinnerets and the adjacent part of the egg sac, fusing the egg sac to the spinnerets. The abdomen with attached egg sac was then immersed directly in 70% ethanol, taken to 100% ethanol as above, then transferred to benzene, which was changed twice over the course of at least a few weeks. The specimen was then air dried, mounted, sputter-coated, and examined. We never settled on a uniform protocol since no one of the variants emerged as clearly superior to the others with all specimens or species, though squeezing the abdomen is most often warranted.

As mentioned, spinnerets on exuvia shed by a few lycosids were also examined by SEM. These were prepared by isolating the spinneret group and sticking it to a carbon adhesive tab on a SEM stub. A small volume of an aqueous solution containing a detergent (to reduce surface tension and increase wettability) was then applied to the spinnerets prior to attempting to uncrumple the spinnerets. We used Laemmli's (1970) sodium dodecyl sulfate electrophoresis sample buffer, diluted to about half strength, for this purpose, though other compositions would no doubt serve at least as well. While immersed in this solution, an insect pin or a tine on a pair of fine forceps was inserted into each spinneret in order to re-expand it and allow its spinning field to be viewed. The spinneret group was then fixed (though this is probably not necessary), dehydrated, treated with HMDS, air dried, mounted, sputter-coated, and examined as described above.

Distinguishing 1° ampullate spigots from 2° ampullate spigots.—In the results presented below, differences between 1° and 2° ampullate fibers and spigots of adult female lycosids are noted. Our interpretation of the relative contributions made by 1° and 2° ampullate glands to egg sac attachment relies on having identified 1° and 2° ampullate spigots correctly. We considered four lines of evidence in making these identifications and, in the manner of Coddington (1989), the same kind of reasoning can be applied to many other spider families. (1) Since 2° ampullate spigots are represented only by ampullate nubbins in adult male lycosids (Figs. 13, 15), their positions relative to the 1° ampullate spigots can be used as a key to distinguishing 1° from 2° ampullate spigots in adult females and juveniles. (2) Because only 2° ampullate glands are functional during proecdysis (right up until the old cuticle is shed from the spinnerets), the only ampullate fibers emerging from spigots on the old cuticle during proecdysis are 2° ampullate fibers (Townley et al. 1993). Consequently, the only ampullate fibers on the exuvium after ecdysis pass through 2° ampullate spigots (Townley et al. 1991:figs. 14–15; Townley et al. 1993:fig. 4). While 2° ampullate fibers do not invariably remain attached to exuvia, they do so with enough regularity that examinations of exuvia can be used to determine which ampullate spigots are 1° and which are 2°. Thus, in our scans of lycosid exuvia, we have only observed ampullate fibers emerging from those spigots that we have identified as 2° ampullate spigots, never from those identified as 1° ampullate spigots (Figs. 8, 10, 19, 20). (3) In general, ampullate tartipores, resulting from openings made to accommodate 2° ampullate gland ducts (see Terminology section above), occur closer to 2° ampullate spigots than 1° ampullate spigots. The ampullate tartipores on lycosid ALS and PMS likewise occur closer to the spigots identified as 2° ampullate spigots (e.g., Figs. 18, 21). (4) The arrangement of MaA and piriform spigots on the ALS of lycosids is essentially the same as in *A. cavaticus* (the same cannot be said of the arrangement of spigots on the PMS where the MiA spigots are located). In this araneid we have observed by dissection that the 2° MaA ducts lead to the more posteriorly placed ampullate spigot on each ALS (Townley et al. 1991, 1993). The spigot identified as the 2° MaA spigot in lycosids likewise occurs posterior to that identified as the 1° MaA spigot.

Definition of first instar.—Downes' (1987) definition for the first instar is followed in this report with subsequent instars numbered accordingly. A spider becomes a first instar as a result of the first ecdysis that produces an exuvium that both has legs and does not remain attached to the spider. In the period



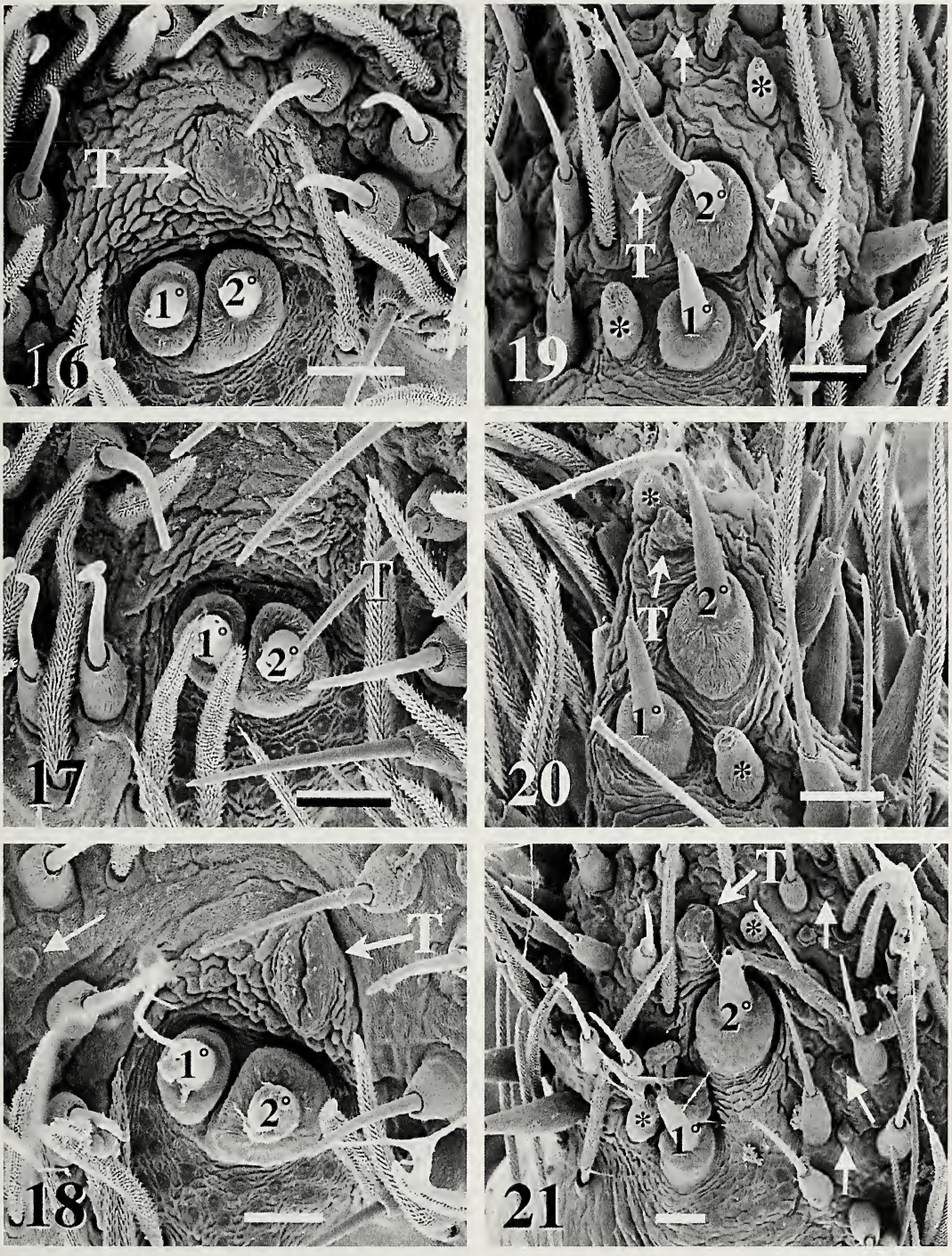
Figures 12–15.—Entire spinning fields on ALS and PMS from a penultimate instar male *Pardosa* sp. and an adult male *Pardosa modica*: 12, 14. Penultimate instar; 13, 15. Adult; 12, 13. Left ALS (posterior at right, lateral at top); 14, 15. Right PMS (posterior at left, lateral at top). Note that 2° MaA and 2° MiA spigots are represented in the adult male only by MaA and MiA nubbins, respectively. Unlabeled arrows point to examples of piriform (Figs. 12–13) or aciniform (Figs. 14–15) tartipores. Scale bars (12, 14) = 10 μm; (13, 15) = 20 μm.

between hatching and the ecdysis that yields a first instar, the spider is a postembryo (Downes 1987).

RESULTS

Abbreviations on micrographs.—AC = attachment cone; C = cylindrical gland spigot; ES = egg sac; N = MaA nubbin (if the spinneret is an ALS) or MiA nubbin (if the spinneret is a PMS); 1° = 1° MaA spigot (on ALS) or 1° MiA spigot (on PMS); 2° = 2° MaA spigot (on ALS) or 2° MiA spigot (on PMS); T = MaA tartipore (on ALS) or MiA tartipore (on PMS); l = left; r = right.

Ampullate gland spigot, nubbin, tartipore complements.—Spinnerets from male and female representatives of three lycosid genera (*Pardosa*, *Gladicosa*, *Trochosa*) were examined, as were those from females only of the genus *Hogna* (Table 3). With one clearly anomalous exception (see Table 3), no variation was seen with regard to the number of ampullate gland spigots/nubbins/tartipores for a given sex at a given stage of development. Assuming these genera present the typical, if not invariable, lycosid condition, adult females and juveniles of both sexes that are at least second instars have two MaA spigots and one MaA tartipore on each ALS (Figs. 8, 9, 12, 16–18, 22, 40, 41) and two MiA spigots and one MiA tartipore on each PMS (Figs. 10, 11, 14, 19–21, 23, 38, 39, 42) (first instars lack tartipores, Figs. 2–5), while adult males have one MaA spigot, one MaA nubbin, and one MaA tartipore on each ALS (Fig. 13) and one MiA spigot, one MiA nubbin, and one MiA tartipore on each PMS (Fig. 15). The 2° MaA and 2° MiA spigots of juvenile males are vestigial in adult males, being represented only by 2° MaA/2° MiA nubbins.



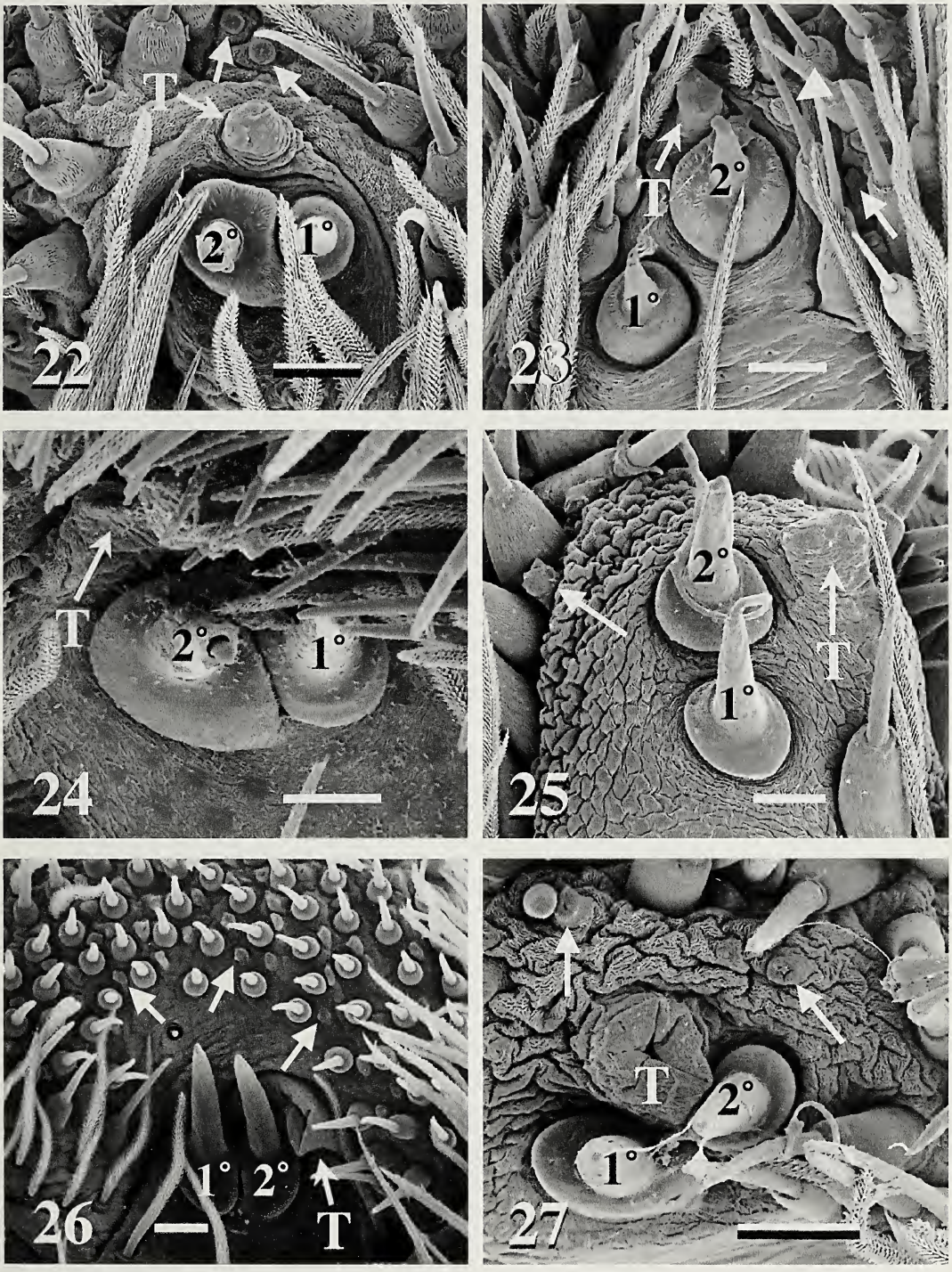
Figures 16–21.—Portions of the ALS and PMS containing the ampullate spigots, from an adult female *Hogna helluo* and the last exuvium shed by this individual (i.e. the cuticle of the penultimate instar), as well as from the last exuvium shed by a female *Hogna* sp. killed while a penultimate instar (i.e. the cuticle of the antepenultimate instar; the same exuvium from which the PLS in Figs. 6–7 was taken): 16, 19. Antepenultimate instar; 17, 20. Penultimate instar; 18, 21. Adult; 16, 17, 18. Left ALS (posterior at right, lateral at top); 19, 21. Left PMS (posterior at right, lateral at top); 20. Right PMS (posterior at left, lateral at top). The MaA tartipore is largely obscured in Fig. 17. Unlabeled arrows point to examples of piriform (Figs. 16, 18) or aciniform (Figs. 19, 21) tartipores. Asterisks (*) identify the two aciniform nubbins on each PMS. Scale bars = 25 μm.

With regard to ampullate spigot/nubbin/tartipore complements, apart from the absence of a MiA nubbin on one PMS in single adult male specimens of *M. asperatus* and *T. oblongus*, no departures from the lycosid condition were observed when viewing spinnerets from the pisaurid (Figs. 24–27), agelenid (Figs. 28, 29), thomisid (Figs. 32, 33), philodromid (Figs. 30, 31), and miturgid (Figs. 34, 35) species listed in Table 3. The same is true of the *C. aerialis* examined. But in an adult female *C. lamellosus*, the number of MaA spigots/nubbins differed between the right and left ALS (Table 3). The formation of a MaA nubbin rather than a 2° MaA spigot on one ALS in this individual again seems to be an example of an anomaly. More significant was the presence of 2° MiA spigots on both PMS (and the absence of 2° MaA spigots on both ALS) of an adult male *C. montanus* (Table 3). This indicates that, in *Coras*, complements differ either interspecifically or intraspecifically. In *P. audax*, adult males, as well as adult females (Figs. 36, 37), retain 2° MaA and MiA spigots (Table 3). This is also the case in the salticid *Philaeus chrysops* (Poda 1761) (Millot 1935) and is consistent with Millot's (1935:509) statement that sexual dimorphism in the spinning apparatus of salticids is negligible. It is, therefore, worth noting that adult male specimens of *S. scenicus* and *Sitticus pubescens* (Fabricius 1775) (one of each species) lacked 2° ampullate spigots (Table 3), though for the latter we have only PMS data. These spigots were represented by nubbins and, in the case of one PMS on the *S. scenicus* individual, it appears that even the nubbin did not form (see 'Occurrence of nubbins' in the introductory section). As an adult female *S. scenicus* did have 2° ampullate spigots (Table 3), it appears that some salticids match the lycosid condition (Table 2) while others do not.

Relative sizes of 1° and 2° ampullate gland spigots.—In early instar lycosids (first and second instar *P. xerampelina*, third instar *T. ruricola*), 1° and 2° MaA spigots are roughly comparable in size, with the bases and shafts of the 1° MaA spigots a little greater in diameter than those of the 2° MaA spigots (Fig. 2). Typically, MiA spigots more clearly differ in size, again with the shafts and bases of 1° MiA spigots wider than those of 2° MiA spigots (Fig. 4). In *Pardosa* of both sexes, the 1° ampullate spigots, especially the 1° MiA spigots (Fig. 14), may retain marginally to moderately greater size through the penultimate instar, or 1° and 2° ampullate spigots may have about the same diameter (Figs. 8, 12). In contrast, in female *Hogna*, it is the 2° ampullate spigots that tend to be larger in the antepenultimate (Figs. 16, 19) and penultimate (Figs. 17, 20) instars. The difference is more pronounced on the ALS, with the bases of the 2° MaA spigots clearly larger than those of the 1° MaA spigots. Also, the difference in size between ampullate spigots and nearby aciniform or piriform spigots is greater in these *Hogna* juveniles than in juvenile *Pardosa*, due, seemingly, to disproportionately larger ampullate spigots (rather than smaller aciniform and piriform spigots) (cf. Figs. 8, 10, 12, 14 with Figs. 16, 17, 19, 20).

With the final molt in female *Pardosa*, the bases of the 2° ampullate spigots become decisively wider than those of the 1° ampullate spigots (cf. Fig. 8 with Fig. 9, and Fig. 10 with Fig. 11, all taken from the same individual). The degree to which this occurs varies noticeably within a species. Nevertheless, it has been apparent in all adult female *Pardosa* that we have examined (Table 3). The relative disparity between 1° and 2° ampullate spigots may also increase after the last molt in female *H. helluo* so that it is perhaps more obvious in adults than in penultimate instars that the bases of the 2° ampullate spigots have greater diameters than those of the 1° ampullate spigots (cf. Fig. 17 with Fig. 18, and Fig. 20 with Fig. 21). However, the changes seen following the last molt in *Hogna* females are certainly not as dramatic as those observed in *Pardosa*. In adult female *G. gulosa* (Figs. 22, 23) and *T. ruricola* (Fig. 43), the bases of the 2° ampullate spigots, especially the 2° MaA spigots, are likewise of greater diameter than the 1° ampullate spigot bases.

Among the adult female pisaurids examined (Table 3), noticeably (but not greatly) wider 2° ampullate spigot bases were observed on the ALS and/or PMS of all three *Dolomedes scriptus* Hentz 1845 (Figs. 24, 25), though one of these had 1° and 2° MaA spigots of essentially the same size while a second spider had 1° and 2° MiA spigots of similar size. There was also little difference in size between 1° and 2° ampullate spigots on the one *D. tenebrosus* Hentz 1844 examined, with 2° spigots



Figures 22–27.—Portions of the ALS and PMS containing the ampullate spigots, from adult females: 22, 23. *Gladicosa gulosa* (Lycosidae); 24, 25. *Dolomedes scriptus* (Pisauridae); 26, 27. *Pisaurina mira* (Pisauridae); 22, 24. Right ALS (posterior at left, lateral at top); 26. Left ALS (posterior at right, lateral at top); 25, 27. Right PMS (posterior at left, lateral at top); 23. Left PMS (posterior at right, lateral at top). Unlabeled arrows point to examples of piriform (Figs. 22, 26) or aciniform (Figs. 23, 25, 27) tartipores. An arrowhead in Fig. 23 points to an aciniform nubbin. Scale bars = 25 μm.

only marginally larger. In *Pisaurina*, 1° and 2° MaA spigots were of about the same size (Fig. 26) and 1° MiA spigots were larger than 2° MiA spigots (Fig. 27).

Among the non-lycosoid adult females examined (Table 3, Figs. 28–37), larger-diameter 2° ampullate spigot bases were observed only on the ALS (and not the PMS) of two thomisids, *M. oblongus* (Figs. 32, 33) and *Misumena vatia* (Clerck 1757). The difference was small and, moreover, in two *M. asperatus* females the 1° MaA spigots were larger than or about the same size as the 2° MaA spigots (not shown). Likewise, in *Agelenopsis* (Figs. 28, 29), *Coras* (not shown), *Tibellus oblongus* (Walckenaer 1802) (Figs. 30, 31), *Cheiracanthium mildei* L. Koch 1864 (Figs. 34, 35), *P. audax* (Figs. 36, 37), and *S. scenicus* (not shown), 2° ampullate spigots were either about the same size as the 1° ampullate spigots or smaller (though in adult *P. audax*, male and female, the 2° ampullate spigots were longer and in the one examined *S. scenicus* adult female, 2° MiA spigots were longer than 1° MiA spigots while 1° and 2° MaA spigots were of about equal length).

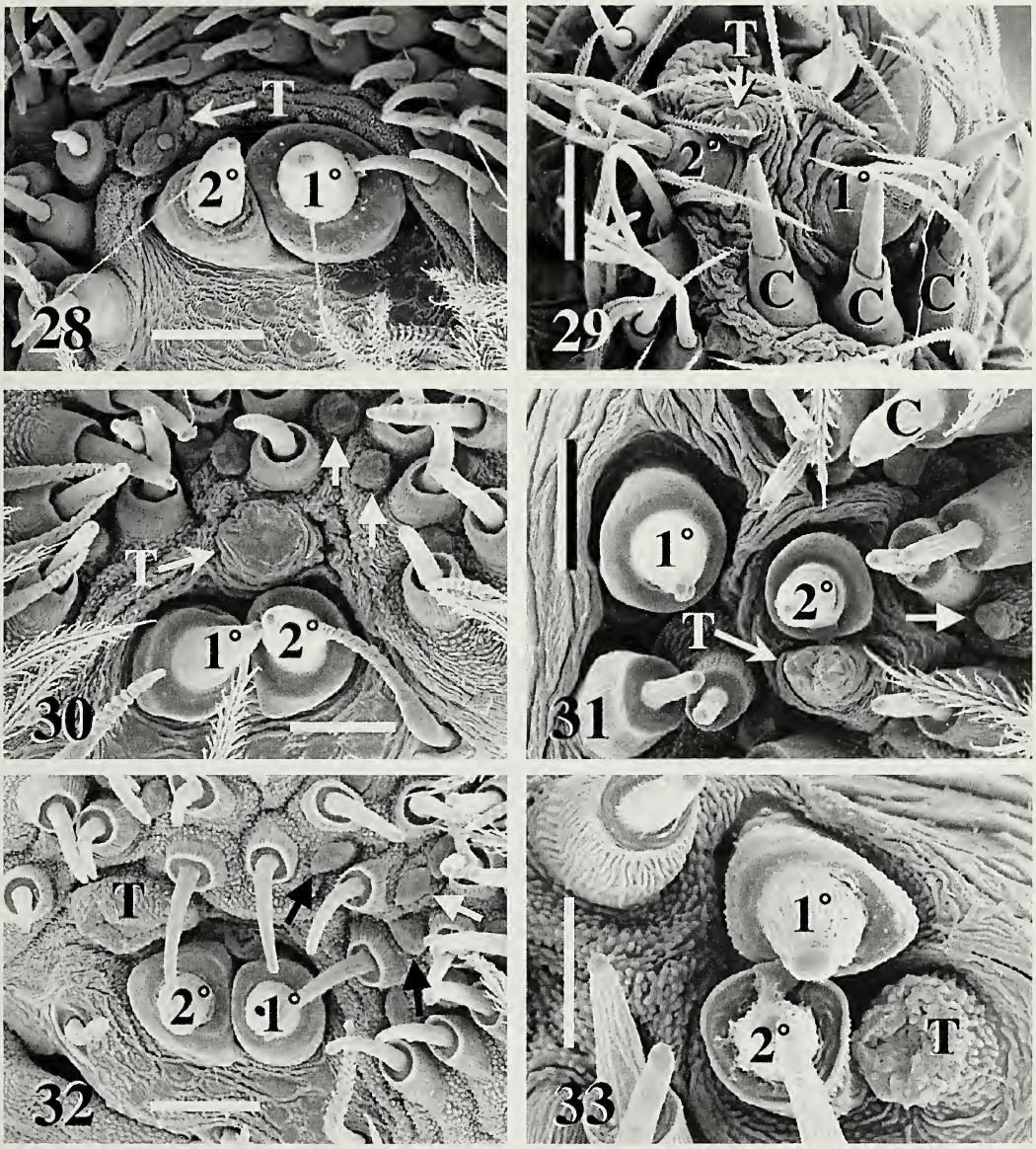
Egg sac attachment.—In the four *Pardosa* species examined with attached egg sacs, eight silk fibers emanating from the 1° and 2° MaA spigots and the 1° and 2° MiA spigots were attached to the egg sac (Figs. 38–42). Likewise, in a single specimen of *T. ruricola*, 1° and 2° MaA fibers at least were used to secure the egg sac to the spinnerets (Fig. 43). We were unable, however, to determine if this individual was also using MiA fibers. In some preparations, single to several piriform fibers accompanied MaA fibers, but in no instances were fibers observed coming from aciniform or cylindrical (= tubuliform) gland spigots, including those on the PLS.

In all five species, 2° ampullate fibers had greater diameters than 1° ampullate fibers (Figs. 38–43, 49). Measurements obtained on some of these fibers from four of these species are presented in Table 4 and, though the data are few, provide an indication of the disparity between 1° and 2° ampullate fibers. In contrast, on the left ALS of one of the examined adult female *D. scriptus*, the 1° MaA spigot was only slightly smaller than the 2° MaA spigot and silk fibers emerging from these spigots had diameters of 2.40 μm and 2.50 μm, respectively. On the left ALS of an adult female *M. asperatus*, the 1° and 2° MaA spigots were about the same size and fibers emerging from them had diameters of 2.47 μm and 2.00 μm, respectively.

Ampullate fibers from the spinnerets are typically attached to the surface of the egg sac by groups of fibers that often take the form of a cone (Figs. 38, 40, 44, 46, 48). The fibers in these "attachment cones" have smaller diameters than the 1° ampullate fibers (Fig. 47 and many of them appear to be fused to one another (Figs. 45, 47). They extend beyond the cone for a short distance on the surface of the egg sac. A single attachment cone secures one or more ampullate fibers to the egg sac. Thus, one (Fig. 44) to several (Figs. 38, 48) cones in close proximity affix the eight ampullate fibers. There appears to be a generic difference with regard to the number of cones that are typically produced (one or two in *Gladicosa* and *Trochosa*, several in *Pardosa*), but more observations are needed to verify this.

Aciniform nubbins.—Though not an objective of this study, a small number of aciniform nubbins were noticed on several lycosid specimens and we think their seemingly non-random occurrence warrants mention. In four female *Hogna* individuals (two adult *H. helluo*, one adult *H. aspersa* (Hentz 1844), one penultimate instar *Hogna* sp.), two aciniform nubbins were observed on each PMS in the vicinity of the MiA spigots. (No male *Hogna* have been examined.) They were also present on the most recent exuvium shed by the penultimate instar (i.e., the cuticle of the antepenultimate instar) and on the last exuvium shed by one of the adult *H. helluo*. One of these nubbins occurs anterior to the 1° MiA spigot, the other lateral or posterolateral to the 2° MiA spigot (Figs. 19–21). In addition, three aciniform nubbins were observed on each PLS, roughly in the middle of the spinning field, in the penultimate instar and its most recent exuvium (Figs. 6, 7), as well as in one adult *H. helluo*. On the other examined *Hogna* cuticles, either one or two aciniform nubbins were found per PLS, though this could be because these PLS preparations were not fully expanded and additional nubbins were obscured.

We have not seen these aciniform nubbins in *Pardosa* or *Trochosa*. In an adult male *G. gulosa*, two aciniform nubbins were on the left PMS in the same positions as in *Hogna*, but only the more lateral of the two was present



Figures 28–33.—Portions of the ALS and PMS containing the ampullate spigots, from adult females: 28, 29. *Agelenopsis naevia* (Agelenidae); 30, 31. *Tibellus oblongus* (Philodromidae); 32, 33. *Misumenops oblongus* (Thomisidae); 28, 32. Right ALS (posterior at left, lateral at top); 30. Left ALS (posterior at right, lateral at top); 29, 31, 33. Right PMS; 29, 33 Posterior at right, lateral at bottom; 31 Posterior at top, lateral at right. Unlabeled arrows point to examples of piriform (Figs. 30, 32) or aciniform (Fig. 31) tartipores. Scale bars (28) = 25 μm; (29) = 50 μm; (30–32) = 15 μm; (33) = 10 μm.

on the right PMS, and none were found on the PLS. Of four adult female *G. gulosa*, one had a single lateral aciniform nubbin on one PMS (Fig. 23) but none on the other PMS or either PLS, while on a second female we could find only one nubbin on one of the PLS. No aciniform nubbins were seen on the spinnerets of the other two females (though on one of these our views of the PMS and PLS were limited as the spinnerets were not well spread).

DISCUSSION

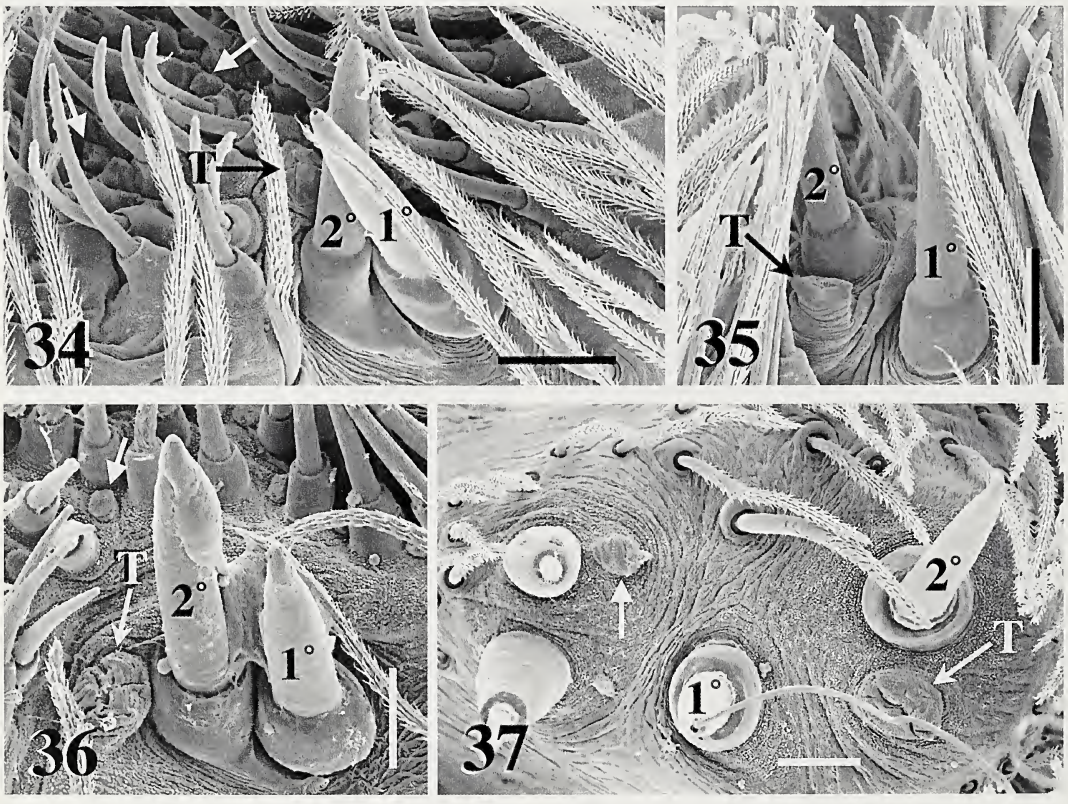
The observations presented in this paper demonstrate that adult females of at least some species of lycosids use 1° and 2° MaA/MiA gland fibers to connect the egg sac to the

Table 4.—Diameters (in μm) of ampullate fibers produced by adult female lycosids for attaching the egg sac to the spinnerets. Measurements were made by SEM at magnifications > 10,000×. *n* = number of individuals from which fibers were measured. For each spider, corresponding fibers from both ALS/PMS were measured and averaged. For *P. moesta* and *P. lapidicina*, the means so obtained for each individual were then used to calculate the overall means ± their standard errors.

Species	*n*	1° MaA fibers	2° MaA fibers	1° MiA fibers	2° MiA fibers
Pardosa moesta Banks 1892	5	0.83 ± 0.038	2.56 ± 0.120	0.76 ± 0.020	2.57 ± 0.171
Pardosa lapidicina Emerton 1885	2	0.99 ± 0.026	3.93 ± 0.319	0.93 ± 0.090	3.86 ± 0.181
Pardosa littoralis Banks 1896	1	0.90	2.86	0.50	2.53
Trochosa ruricola (De Geer 1778)	1	1.31	3.06		

spinnerets. Given the greater diameter of the 2° ampullate fibers (Table 4), they presumably constitute the more indispensable part of this tether.

Egg sac attachment in lycosids versus trechaleids and rhoicinines.—In contrast to *Pardosa* females that use both MaA and MiA fibers (1° and 2°) for attaching the egg sac, for a total of eight ampullate fibers, Carico (1993) reports that trechaleid females use only MiA fibers (but, again, both 1° and 2°; see his fig. 4) for this purpose, for a total of four ampullate fibers. And while 2° ampullate fibers are considerably wider than 1° ampullate fibers in



Figures 34–37.—ALS and PMS from adult females: 34, 35. *Cheiracanthium mildei* (Miturgidae); 36, 37. *Phidippus audax* (Salticidae); 34, 36. Portion of right ALS containing the MaA spigots (posterior at left, lateral at top); 35. Portion of left PMS containing the MiA spigots (posterior at right, lateral at top); 37. Left PMS, entire spinning field shown (two MiA and two aciniform spigots) (posterior at right, lateral at top). Unlabeled arrows point to examples of piriform (Figs. 34, 36) or aciniform (Fig. 37, the only one) tartipores. Scale bars = 25 μm.

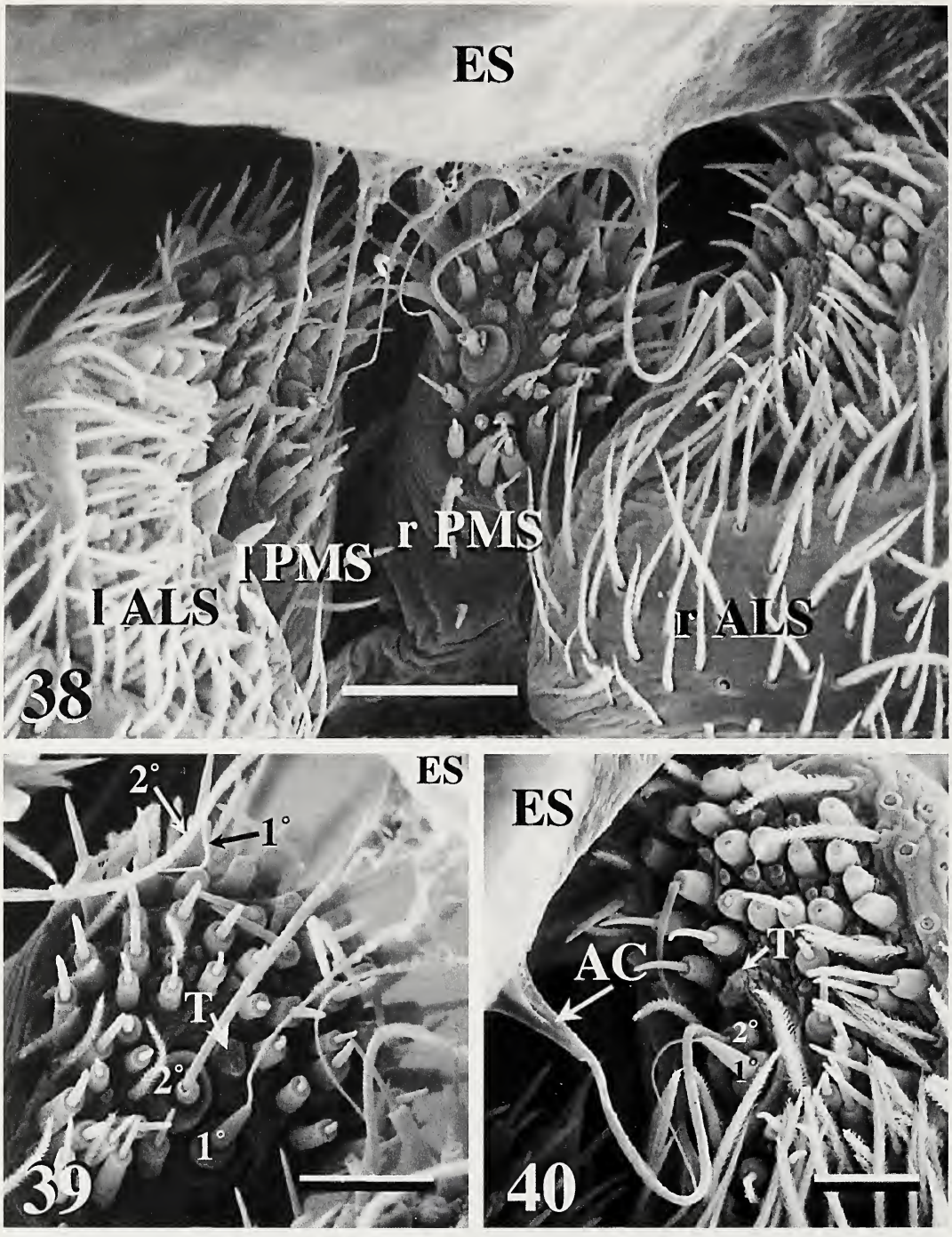
Pardosa and *Trochosa* (at least on the ALS of the latter, Table 4), the 1° and 2° MiA fibers of *Hesydrus*, shown in fig. 4 of Carico (1993), do not appear to differ substantially in diameter. Carico (1993:230) describes these trechaleid MiA fibers as 'strong' and this seems apt considering that our measurements of 2° ampullate fiber diameters in *Pardosa*, *Trochosa*, and *Dolomedes* were in the range of about 2.3–4.4 μm, whereas the MiA fibers in Carico's fig. 4 have diameters of about 9–12 μm. Thus, what the trechaleid tether lacks in number of fibers is perhaps more than made up for in strength per fiber. Additional comparisons between these two families are made in the appropriate sections below.

In contrast to lycosids and trechaleids, it has been reported that *Rhoicinus* and *Rhoicinaria* (the latter currently placed in Amaurobiidae, see Platnick 2002) carry their egg sacs attached to the posterior spinnerets; i.e., the PLS (see Exline 1950, 1960). If true, attachment is presumably accomplished using fibers from aciniform and/or cylindrical glands, rather than ampullate gland fibers.

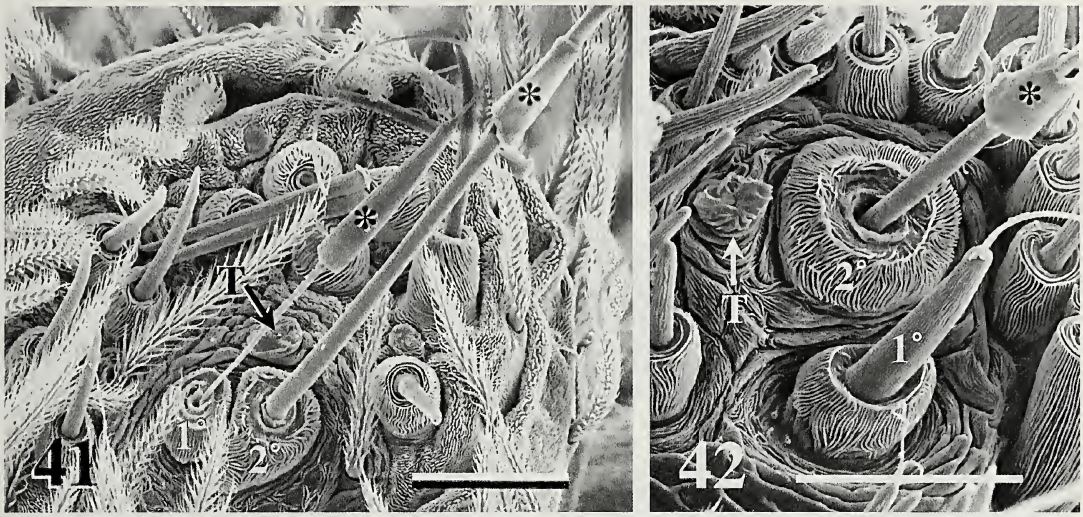
Ampullate glands in lycosids versus araneoids.—To us, the female lycosid's (or trechaleid's) use of 2° ampullate silk is most interesting when compared with the araneoid condition. The evidence to date indicates that 2° ampullate glands produce silk in araneoids only during proecdyses (Townley et al. 1993) and, therefore, these glands are not needed and not functional in adults of either sex. What occurs in adult female lycosids (and adult females from some other families, Tables 2, 3) appears to be a variation on this scheme. As in araneoids, the 2° ampullate glands of juvenile lycosids apparently produce silk during proecdyses. This is indicated by the presence of ampullate tartipores in second instar through adult lycosids and is consistent with the replacement of 2° ampullate spigots by 2° ampullate nubbins in adult males (Table 3; Figs. 1, 12–15). In araneoids, the final molt differs from the preceding molts, with regard to the ampullate glands, in that the blocked 2° ampullate glands present in the last juvenile instar (see Table 1) remain blocked and do not re-develop in the adult. And because the open 2° ampullate glands present in the last juvenile instar become blocked and regress in the adult, as they do after each molt, the adult contains two sets of blocked 2° ampullate glands, rather than one blocked set and one open set (as in juveniles). From our observations on spinnerets, we infer that this difference between the final molt and all preceding molts does not exist in female lycosids (among others). That is, the blocked 2° ampullate glands present in a penultimate instar female lycosid do become open 2° ampullate glands in the adult and re-develop accordingly (Fig. 1). Presumably, they are not functional immediately after the last ecdysis, requiring at least a day or two to re-develop and accumulate luminal contents, but would thereafter be able to produce silk fibers concurrently with the 1° ampullate glands.

On the other hand, it would seem that the 2° ampullate glands of female lycosids (*Pardosa* at least) are not completely unresponsive to the hormonal changes that culminate in an adult being produced, as evidenced by the enlarged 2° ampullate spigots of adults (e.g., Figs. 9, 11). And given the greater diameters of 2° ampullate fibers in adult females (relative to the 1° ampullate fibers), there may also be internal changes to the 2° ampullate glands, such as substantial increases in the calibers of their ducts, that occur at the same time.

Other functions of 2° ampullate gland fibers.—Though we have only observed 2° ampullate fibers being used for egg sac attachment, we are not suggesting that this is the only role the 2° ampullate glands play in the adult female. Instead, it may be that when these spiders are not carrying egg sacs, fibers from these glands are used for other purposes. One possibility is that they contribute to the dragline. Such an application of 2° ampullate silk may be especially significant for species in which adult female draglines stimulate courtship behaviors in adult males (reviewed in Tietjen & Rovner 1982; also, e.g., Stratton & Uetz 1983; Lizotte & Rovner 1989; Hebets et al. 1996; Fernández-Montraveta & Ruano-Bellido 2000). As in egg sac attachment, the greater diameter of these fibers might also make them better suited to this role than the 1° ampullate fibers. Mechanically, the 2° ampullate fibers would present a more substantial trail that might be more easily discerned by males and, from a chemosensory perspective, the greater surface area of a 2° ampullate fiber has greater potential for presenting pheromones to males. Considering that 2° ampullate spigots (implying functional 2° ampullate



Figures 38–40.—Spinnerets with attached egg sac in adult female *Pardosa modica*: 38. 1° and 2° MaA fibers from both ALS and 1° and 2° MiA fibers from both PMS are attached to the egg sac; 39. Left PMS from the same preparation, showing more clearly the emergence of fibers from the MiA spigots, as well as 1° and 2° MaA fibers from the left ALS in the upper left corner; 40. Right ALS from the same preparation, showing the emergence of fibers from the MaA spigots. The MaA fibers from this ALS are attached to the egg sac by a well-defined (and undamaged) attachment cone. Note that the 2° ampullate fibers have considerably greater diameters than the 1° ampullate fibers. The PLS are out of the field of view in Fig. 38 (no fibers were observed coming from the PLS). Scale bars (38) = 100 μm; (39, 40) = 50 μm.



Figures 41–42.—Ampullate fibers used for egg sac attachment in *Pardosa littoralis* (posterior at right, lateral at top): 41. Portion of left ALS showing 1° and 2° MaA fibers; 42. Portion of left PMS showing 1° and 2° MiA fibers. Both micrographs were taken after the egg sac was removed from the spinnerets. In preparing the spider for SEM (before the egg sac was removed), the shafts (*) of both MaA spigots and the 2° MiA spigot became detached from the bases. Scale bars = 25 μm.

glands) are present in adult females belonging to several other families in which egg sacs are not carried on the spinnerets (Tables 2, 3), and assuming fibers from these spigots play a useful role(s) in such females, it would seem likely that adult female lycosids use 2° ampullate fibers for purposes in addition to egg sac transport. On the other hand, the greater material and energetic cost of producing the larger-diameter 2° ampullate silk may limit its use in other applications.

Comparative ampullate gland spigot morphology.—After observing the relatively large 2° ampullate spigots of adult female lycosids, we were curious to know if this feature is unique to lycosids, or perhaps to lycosids, trechaleids, and rhoicinines. Such a limited occurrence would more strongly suggest that the mode of egg sac transport used by these spiders may have been made possible by or facilitated by selection for enlarged 2° ampullate spigots from which relatively large-diameter 2° ampullate fibers are drawn. And in this context, might this feature extend to pisaurids as well? Several authors have noted that adult female pisaurids transport their egg sacs, held under the sternum, using not only their chelicerae and palps, but also silk from the spinnerets (e.g., Lécaillon 1905:137; Bishop 1924:27–28; Nielsen 1932:133, 135; Bristowe 1958:187, 190; Dondale & Redner 1990: 322; Carico 1976:63, 1993:235–236), and Carico (1993) has suggested that egg sac transport using the spinnerets is plesiomorphic for lycosids, trechaleids, and pisaurids. This raises the possibility that ampullate silk may also play a role, albeit a less crucial one, in egg sac transport in the Pisauridae. On the other hand, Roberts (1995:236) has ". . . never seen any threads running between the sac and the spinners . . . " in pisaurids, which points up the desirability of investigating the extent and nature of silk use in egg sac transport within this family. Or are relatively large 2° ampullate spigots unrelated to egg sac transport, with such spigots routinely encountered among those entelegynes that retain 2° ampullate spigots as adults, yet do not use ampullate silk for egg sac transport? Questions such as these prompted us to begin examining, as opportunities have arisen, spinnerets of such non-lycosid entelegynes.

At present, our survey is very limited (Table 3) and needs to be expanded, including examining more lycosids and other lycosoids. Thus, we lack satisfactory answers to the above questions. As detailed below, from what data we have and from observations reported in the literature, it seems that 2° ampullate spigots are generally not larger than 1°

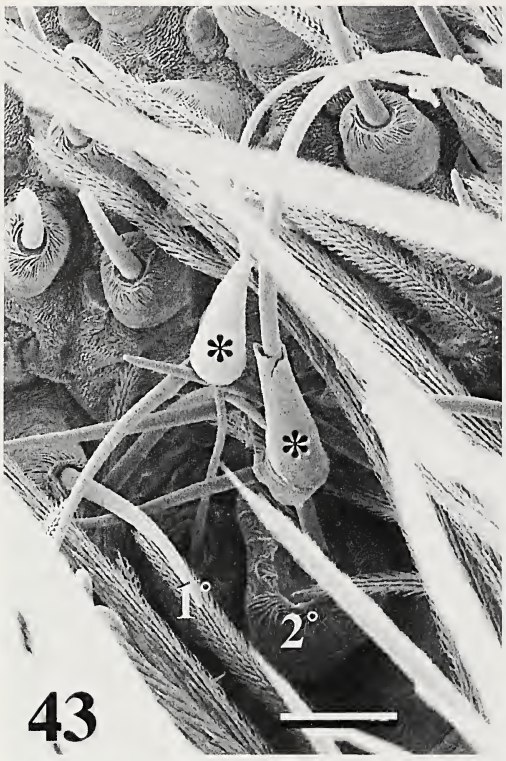


Figure 43.—Portion of left ALS containing the MaA spigots (posterior at right, lateral at top), showing MaA fibers that were being used for egg sac attachment in *Trochosa ruricola*. The micrograph was taken after the egg sac was removed from the spinnerets. As in Fig. 41, the shafts (*) of both MaA spigots became detached from the bases while processing the specimen for SEM. Scale bar = 20 μm.

ampullate spigots among entelegynes. But on the other hand, larger 2° ampullate spigots are neither restricted to lycosoids, nor are they present in all lycosoids that use spinnerets, solely or in part, to carry the egg sac. Among the examined non-lycosoids in this study (Figs. 28–37, Table 3), 2° ampullate spigots tended to be smaller or about the same size as 1° ampullate spigots.

This description also applies to the MaA spigots of several amaurobioids (sensu Griswold et al. 1999). Davies (1998b:74) has noted that in *Tasmarubrius* (Amaurobiidae) the ALS of an adult female has two MaA spigots, with the anterior one, i.e. the 1° MaA spigot, larger. Wang (2000) provides micrographs of ALS from several adult female amaurobiids, including *Rubrius* and *Callobius* in which the two MaA spigots appear similar in size. A micrograph of a *Coelotes* right ALS in the same paper (Wang 2000:fig. 4) indicates that the 2° MaA spigot is larger than the 1° MaA spigot, but because the position of the MaA tartipore in the *Callobius* figure indicates the right ALS, rather than the left ALS as stated in the caption, it may be that the figured *Coelotes* spinneret is actually the left ALS, in which case the 1° MaA spigot is larger. In a description of the amaurobioid subfamily Kababininae, Davies & Lambkin (2000a) state that the two MaA spigots on the female ALS are of unequal size. From their fig. 5C of a right ALS in *Malarina*, it appears that the 1° MaA spigot is again larger. And in several amphinectids, 1° MaA spigots are larger than 2° MaA spigots in adult females. Davies (1998a), in describing a *Quemusia* species, states that the anterior MaA spigot (i.e., the 1°) is "much larger" than the posterior MaA spigot (2°), and, in both a *Magua* species and a *Buyina* species, reports that the anterior MaA spigot is larger than the posterior one. 1° and 2° MaA spigots of similar size can be seen on an ALS of an adult female *Liocranoides* (Tengellidae) in fig. 3 of Platnick (1999).

In contrast, several published micrographs demonstrate that larger 2° ampullate spigots, even if not prevalent, are not unique to lycosoids. In fig. 11 of Harvey (1995), an ALS from the nicodamid *Ambicodamus* is shown on which the 2° MaA spigot is conspicuously wider than the 1° MaA spigot. Larger 2° ampullate spigots also occur in some lamponids (Platnick 2000: *Lamponina* ALS, figs. 287 & 288; *Lamponella* ALS, figs. 354 & 355; female *Centrothele* PMS, figs. 408 & 409).

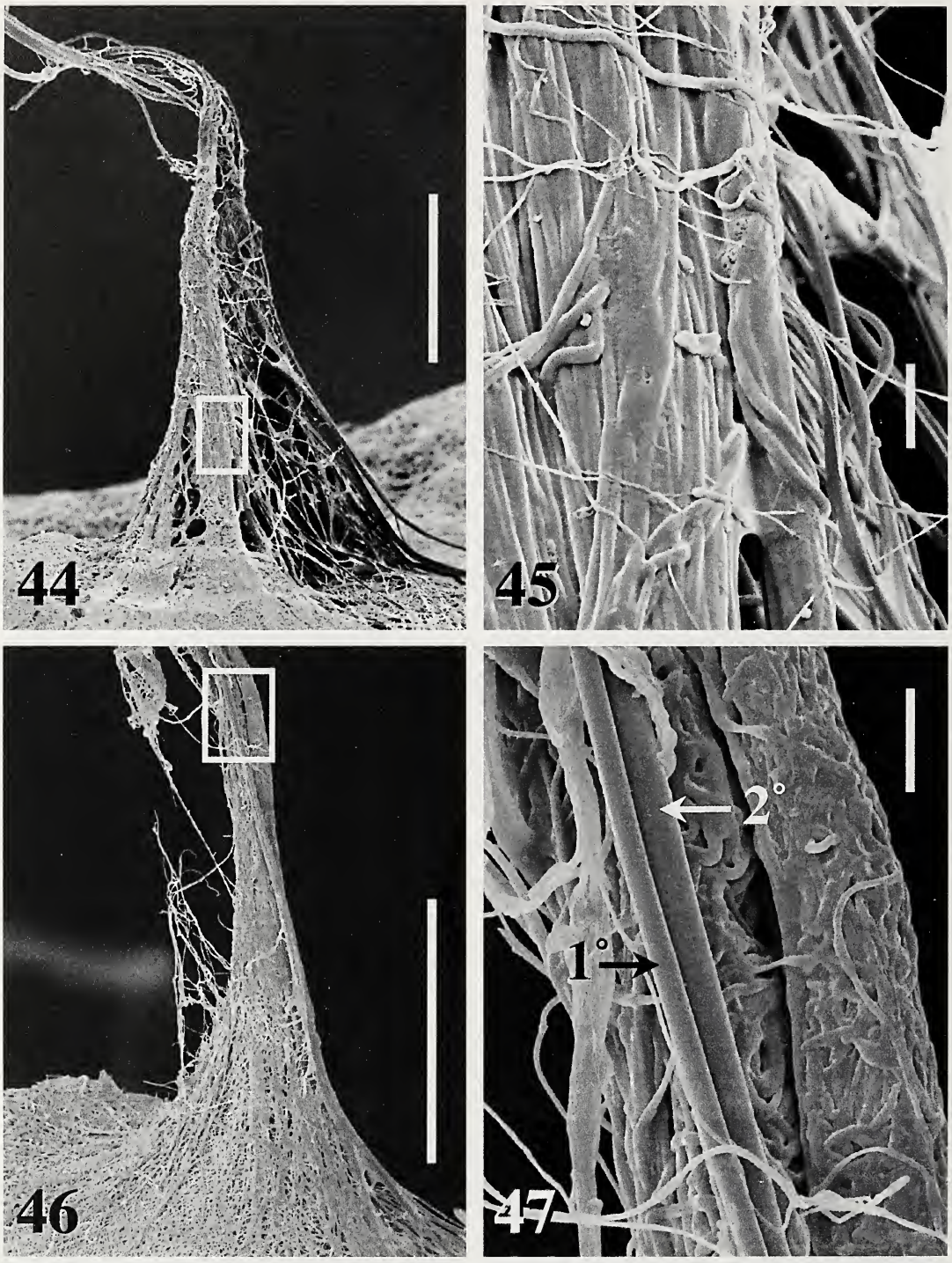
Among the pisaurids examined we saw examples of 2° ampullate spigots that were smaller than, or about equal in size to, 1° ampullate spigots (*Pisaurina*, Figs. 26, 27), as well as examples of 2° ampullate spigots that were noticeably larger than their 1° counterparts (some, though not all, *Dolomedes*, Figs. 24, 25). If enlarged 2° ampullate spigots in lycosids are part of an adaptation facilitating egg sac transport using the spinnerets, then these mixed observations may be a reflection of the supplemental role, at most, that ampullate silk plays in pisaurid egg sac transport. If ampullate silk is not used by pisaurids for egg sac transport, then examples of larger 2° ampullate spigots in pisaurids might simply reflect phylogenetic relatedness between lycos-

ids and pisaurids (e.g., Dondale 1986; Griswold 1993; Silva Davila in press).

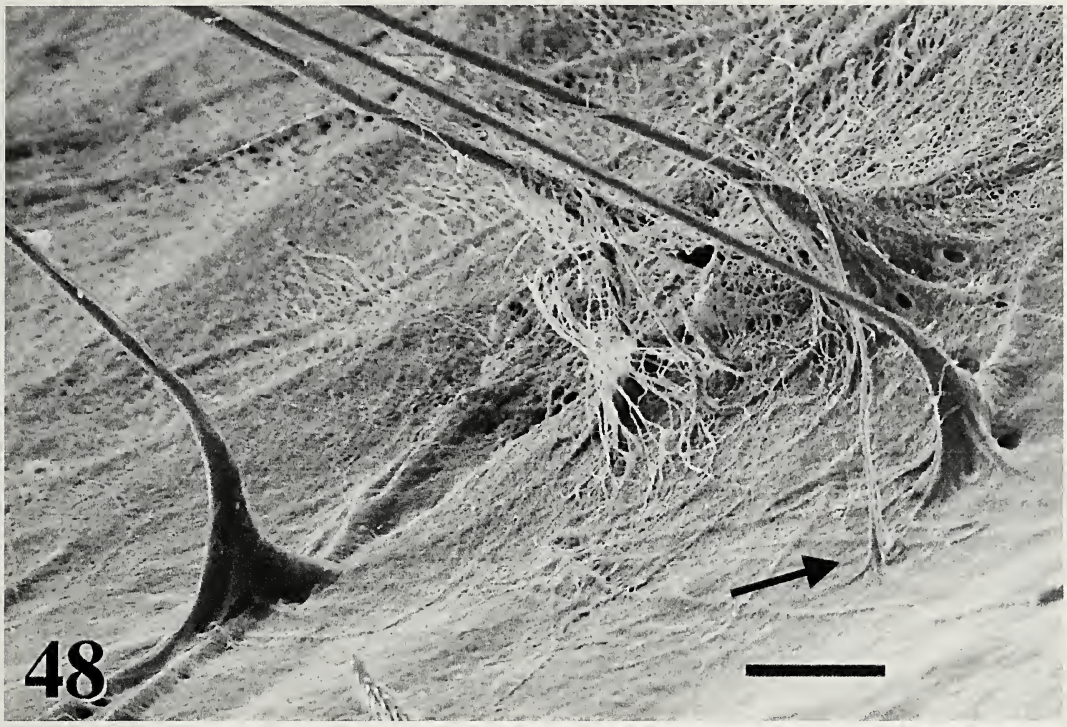
Given our observations on spinnerets from lycosids and pisaurids, and considering that data obtained thus far suggest the Trechaleidae as sister group to the Lycosidae (Sierwald 1990b, 1993; Griswold 1993) or to Lycosidae + Pisauridae (Silva Davila in press), we would have expected 2° ampullate spigots to be larger than 1° ampullate spigots in trechaleids (at least with the MiA spigots since these are used for egg sac attachment (Carico 1993)). But in Carico's (1993) fig. 4 of a *Hesydrus* PMS the 2° MiA spigot (to the right of the 1° MiA spigot in this figure, above the MiA tartipore) does not appear to be larger than the 1° MiA spigot. It may, in fact, be smaller. As mentioned above, the fibers emerging from these spigots also do not differ conspicuously in diameter. But both fibers are very wide, relative to those that we have measured in *Pardosa*, *Trochosa*, and *Dolomedes*, and both spigots are large relative to the aciniform and cylindrical spigots that surround them. There is the possibility, therefore, that trechaleids (*Hesydrus* at least) do have enlarged 2° MiA spigots, but that it is not immediately obvious because the 1° MiA spigots are also enlarged. Since only MiA fibers are used by trechaleids for egg sac attachment (Carico 1993), it would be of value to examine the MaA spigots to see if they and the silk fibers they produce are noticeably smaller than their MiA counterparts. The larger diameters of trechaleid MiA fibers, compared with lycosid and pisaurid ampullate fibers, lead us to speculate that this difference may be related to a behavioral difference among the three families. If an egg sac becomes detached, lycosid and pisaurid females will reattach it, while trechaleid females will not (Carico et al. 1985; Carico 1993). Nor, incidentally, do *Shinobius* (Rhoicininae) females reattach a detached egg sac (Kaihotsu 1988: 17). Do the larger-diameter trechaleid fibers make detachment and, thus, the need for reattachment less likely than among lycosids and pisaurids? The possibility was raised above that the greater cost to a spider of producing larger-diameter fibers may result in more restricted use of such fibers. Thus, do adult female trechaleids use MiA silk exclusively or primarily for egg sac attachment? Again, additional observations are clearly needed.

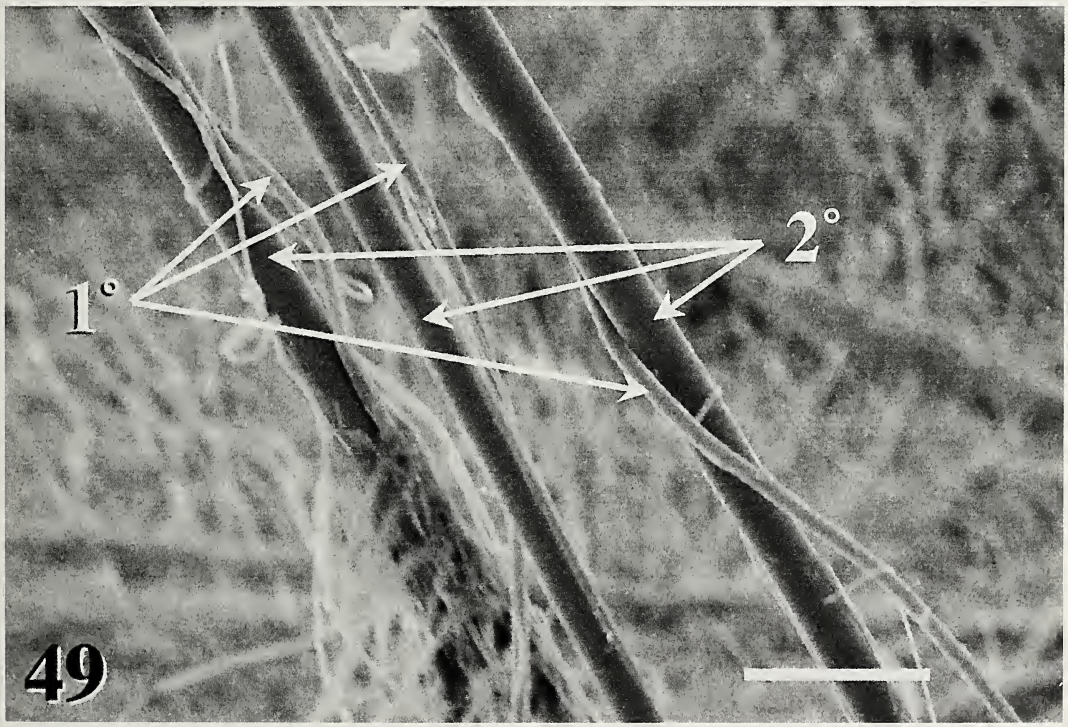
The only scans of rhoicinine spinnerets we have seen are those presented in the description of *Heidrunea* (Brescovit & Höfer 1994). In fig. 6c of Brescovit & Höfer (1994), both PMS of an adult female are shown. We tentatively identify the tartipore, present on each PMS and located just posterior to the three most anterior spigots, as a MiA tartipore. The two spigots immediately posterior to this tartipore are presumably the MiA spigots, with the 2° MiA spigot and MiA tartipore juxtaposed. If these identifications are correct, then the bases of the 1° MiA spigots are wider than those of the 2° MiA spigots. The significance of this observation to any correspondence between the size of 2° ampullate spigots and the use of ampullate silk in egg sac transport, is unknown at present since we do not know if *Heidrunea* attach their egg sacs to their spinnerets and, if they do, if ampullate gland fibers are used. Recall that *Rhoicinus* have been reported to attach egg sacs to the PLS (Exline 1950, 1960), indicating that ampullate gland silks are not involved.

As an aside, we note that amaurobiids of the genera *Amaurobius* and *Callobius* are not included in Table 2 even though Hajer's (1990) observations indicate that they conform to the description given in the table legend. This is because others have reported only a single MiA spigot on each PMS in adult females of these two genera (Platnick et al. 1991:62, 64; Griswold et al. 1999; Wang 2000; the latter contains SEM scans of their PMS), and our own observations on a single specimen of an adult female *Callobius bennetti* (Blackwall 1846) coincide with these later reports. Thus, the 2° ampullate spigot sexual dimorphism considered in Table 2 seems to apply to the 2° MaA spigots only. Such is the situation observed in the amaurobiid genus *Tasmarubrius* (Davies 1998b) and in the amaurobioid subfamily Kababininae (Davies 1999; Davies & Lambkin 2000a, b). Even this more limited sexual dimorphism is absent in some genera currently included (some very tentatively) in the Amaurobiidae (Platnick 2002) given that adult females of *Storenosoma*, *Otira*, *Midgee*, *Manjala*, *Malala* (Davies 1999; Davies & Lambkin 2001), and *Retiro* (Griswold et al. 1999) have only a single MaA



Figures 44–47.—Attachment cones that affix ampullate fibers to the surface of the egg sac: 44, 45. From a *Gladicosa gulosa* egg sac, with the boxed area in Fig. 44 shown at higher magnification in Fig. 45; 46, 47. From a *Trochosa ruricola* egg sac, with the boxed area in Fig. 46 shown at higher magnification in Fig. 47. On the *G. gulosa* egg sac, it appeared that all the ampullate fibers were attached by this one cone, while on the *T. ruricola* egg sac, one 1°/2° pair of ampullate fibers was attached by a separate, more poorly formed or damaged cone. In Figs. 45, 47 note the fusion among many of the fibers that constitute the cones. Scale bars (44, 46) = 100 μm; (45, 47) = 5 μm.





Figures 48–49.—Surface of a *Pardosa moesta* egg sac, at the site where the eight ampullate fibers coming from the ALS and PMS are attached. 48. Each 2° ampullate fiber (the four thickest, most obvious fibers in the micrograph) is attached by a separate attachment cone, one of which is not well-defined or is damaged. Only two of the 1° ampullate fibers are affixed in the same cone as their 2° counterpart. An arrow points to the site where one 1° ampullate fiber is affixed by its own very small cone. 49. The six more closely spaced ampullate fibers from Fig. 48 are shown at higher magnification so that the 1° fiber accompanying each 2° fiber can be seen more clearly. Scale bars (48) = 25 μm; (49) = 10 μm.

spigot on each ALS, accompanied by a MaA nubbin.

Ampullate fiber attachment to the egg sac.—We have not made a specific attempt to determine the glandular origin of the principal fibers that form the cone-like structures by which ampullate fibers are affixed to the surface of the egg sac. Casual observations from SEM micrographs suggest the piriform glands as the most likely candidates. Among females with egg sacs, the only fibers we have observed emerging from spigots are ampullate and piriform fibers. Also, fusion among fibers seen on cones is reminiscent of the fusion that has been described among piriform fibers from webs of *C. citricola* (Peters 1993). It must be acknowledged, however, that fusion has also been observed among other fiber types, including aciniform-A fibers from at least some uloborids (Peters & Kovoor 1989) and cylindrical fibers from *A. aurantia* (Stubbs 1991; Stubbs et al. 1992; Foradori et al. 2002). A role in attaching ampullate fibers to the egg sac surface is consistent with the piriform glands' well known function of producing attachment discs that secure ampullate fibers to various substrates (e.g., Apstein 1889; Warburton 1890; Richter et al. 1971).

From descriptions of trechaleid egg sacs in Sierwald (1990a:8–9; 1993:62), Brescovit et al. (2000:14), and especially Carico (1993: 230, 236), and from figs. 5–6 in the latter paper, it appears that a single attachment cone secures the four MiA fibers to the surface of the egg sac in at least several genera within this family. A single cone may also affix the eight ampullate fibers to the egg sac in some lycosids (e.g., *Gladicosa*), but others (*Pardosa*) typically produce several closely spaced cones that serve to attach these ampullate fibers.

ACKNOWLEDGMENTS

Partial financial support for this work was contributed by Joel Tillinghast. Matthew Foradori (Zoology Department, UNH) and Mesbah Creitz collected some of the spiders used in this study, Margaret Tillinghast made translations from the French, Tomoko Kakazu made a translation from the Japanese, and Joseph Danahy and Douglas Prince (UNH Computing and Information Services) helped ready the figures for publication. Nancy Cherim (UNH EM Facility) was extremely accommodating in making much time on the SEM available to us. Figure 1 was produced at the suggestion of Dr. Jonathan Coddington (National Museum of Natural History, Smithsonian Institution) with additional design suggestions made by Dr. Gail Stratton (University of Mississippi) and Charlene Newton. Drs. Stratton and Coddington and an anonymous reviewer made a number of recommendations that greatly improved the text. Dr. Petra Sierwald (Field Museum of Chicago) identified and determined the sex of juvenile *P. mira* examined in this study and Dr. Charles Dondale (Eastern Cereal & Oilseed Research Centre, Agriculture Canada) identified the examined *Coras* individuals. Diana Silva Davila kindly sent us a copy of her in press manuscript. To all these individuals we are indebted and very grateful.

LITERATURE CITED

Apstein, C. 1889. Bau und Function der Spinndrüsen der Araneida. Archiv für Naturgeschichte 55: 29–74.

Barth, F.G., S. Komarek, J.A.C. Humphrey & B. Treidler. 1991. Drop and swing dispersal behavior of a tropical wandering spider: experiments and numerical model. Journal of Comparative Physiology A 169:313–322.

Bishop, S.C. 1924. A revision of the Pisauridae of the United States. New York State Museum Bulletin 252:4–140.

Bleher, B. 2000. Development of web-building and spinning apparatus in the early ontogeny of *Nephila madagascariensis* (Vinson, 1863) (Araneae: Tetragnathidae). Bulletin of the British Arachnological Society 11:275–283.

Bond, J.E. 1994. Seta-spigot homology and silk production in first instar *Antrodiaetus unicolor* spiderlings (Araneae: Antrodiaetidae). Journal of Arachnology 22:19–22.

Brady, A.R. 1979. Nearctic species of the wolf spider genus *Trochosa* (Araneae: Lycosidae). Psyche 86:167–212.

Brady, A.R. 1986. Nearctic species of the new wolf spider genus *Gladicosa* (Araneae: Lycosidae). Psyche 93:285–319.

Brescovit, A.D. & H. Höfer. 1994. *Heidrunea*, a new genus of the spider subfamily Rhoicininae (Araneae, Trechaleidae) from central Amazonia, Brazil. Andrias 13:71–80.

Brescovit, A.D., J. Raizer & M.E.C. Amaral. 2000. Descriptions and notes on the genus *Paradossenus* in the neotropical region (Araneae, Trechaleidae). Journal of Arachnology 28:7–15.

Bristowe, W.S. 1958. The World of Spiders. Collins Clear-Type Press, London.

Carico, J.E. 1972. The nearctic spider genus *Pisaurina* (Pisauridae). Psyche 79:295–310.

Carico, J.E. 1973. The nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). Bulletin of the Museum of Comparative Zoology 144:435–488.

Carico, J.E. 1976. The spider genus *Tinus* (Pisauridae). Psyche 83:63–78.

Carico, J.E. 1993. Revision of the genus *Trechalea* Thorell (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the Western Hemisphere. Journal of Arachnology 21:226–257.

Carico, J.E., J. Adis & N.D. Penny. 1985. A new species of *Trechalea* (Pisauridae: Araneae) from Central Amazonian inundation forests and notes on its natural history and ecology. Bulletin of the British Arachnological Society 6:289–294.

Chamberlin, R.V. & W. Ivie. 1941. North American Agelenidae of the genera *Agelenopsis*, *Calilena*, *Ritalena* and *Tortolena*. Annals of the Entomological Society of America 34:585–628.

Coddington, J.A. 1989. Spinneret silk spigot morphology: evidence for the monophyly of orbweaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. Journal of Arachnology 17:71–95.

Coddington, J.A. 1990. Cladistics and spider classification: araneomorph phylogeny and the monophyly of orbweavers (Araneae: Araneomorphae; Orbiculariae). Acta Zoologica Fennica 190:75–87.

Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22:565–592.

Davies, V.T. 1993. A new spider genus (Araneae: Amaurobioidea) from rainforests of Queensland, Australia. Memoirs of the Queensland Museum 33:483–489.

Davies, V.T. 1998a. A revision of the Australian metaltellines (Araneae: Amaurobioidea: Amphinectidae: Metaltellinae). Invertebrate Taxonomy 12:211–243.

Davies, V.T. 1998b. A redescription and renaming of the Tasmanian spider *Amphinecta milvina* (Simon, 1903), with descriptions of four new species (Araneae: Amaurobioidea: Amaurobiidae). Pp. 67–82. *In* Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. (P.A. Selden, ed.). British Arachnological Society, Burnham Beeches, Bucks.

Davies, V.T. 1999. *Carbinea*, a new spider genus from North Queensland, Australia (Araneae, Amaurobioidea, Kababininae). Journal of Arachnology 27:25–36.

Davies, V.T. & C.L. Lambkin. 2000a. *Malarina*, a new spider genus (Araneae: Amaurobioidea: Kababininae) from the wet tropics of Queensland, Australia. Memoirs of the Queensland Museum 45:273–283.

Davies, V.T. & C. Lambkin. 2000b. *Wabua*, a new spider genus (Araneae: Amaurobioidea: Kababininae) from North Queensland, Australia. Memoirs of the Queensland Museum 46:129–147.

Davies, V.T. & C. Lambkin. 2001. A revision of *Procambridgea* Forster & Wilton, (Araneae: Amaurobioidea: Stiphidiidae). Memoirs of the Queensland Museum 46:443–459.

Dondale, C.D. 1986. The subfamilies of wolf spiders (Araneae: Lycosidae). Pp. 327–332. *In* Actas X Congreso Internacional de Aracnología, Jaca, España, Vol. 1. (J.A. Barrientos, ed.). Instituto Pirenaico de Ecología y Grupo de Aracnología.

Dondale, C.D. & J.H. Redner. 1978. The Crab Spiders of Canada and Alaska (Araneae: Philodromidae and Thomisidae) (The Insects and Arachnids of Canada, Part 5). Agriculture Canada Publication 1663.

Dondale, C.D. & J.H. Redner. 1982. The Sac Spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae) (The Insects and Arachnids of Canada, Part 9). Agriculture Canada Publication 1724.

Dondale, C.D. & J.H. Redner. 1990. The Wolf Spiders, Nurseryweb Spiders, and Lynx Spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae) (The Insects and Arachnids of Canada, Part 17). Agriculture Canada Publication 1856.

Downes, M.F. 1987. A proposal for standardization of the terms used to describe the early development of spiders, based on a study of *Theridion rufipes* Lucas (Araneae: Theridiidae). Bulletin of the British Arachnological Society 7:187–193.

Engelhardt, W. 1964. Die mitteleuropäischen Arten der Gattung *Trochosa* C.L. Koch, 1848 (Araneae, Lycosidae). Morphologie, Chemotaxonomie, Biologie, Autökologie. Zeitschrift für Morphologie und Ökologie der Tiere 54:219–392.

Exline, H. 1950. Spiders of the Rhoicininae (Pisauridae) from western Peru and Ecuador. American Museum Novitates 1470:1–13.

Exline, H. 1960. Rhoicinine spiders (Pisauridae) of western South America. Proceedings of the California Academy of Sciences, Fourth Series 29: 577–620.

Fernández-Montraveta, C. & J. Ruano-Bellido. 2000. Female silk and mate attraction in a burrowing wolf-spider (Araneae, Lycosidae). Bulletin of the British Arachnological Society 11: 361–366.

Foradori, M.J., J. Kovoor, M.-J. Moon & E.K. Tillinghast. 2002. Relation between the outer cover of the egg case of *Argiope aurantia* (Araneae: Araneidae) and the emergence of its spiderlings. Journal of Morphology 252:218–226.

Forster, R.R. 1967. The Spiders of New Zealand, Part I. Otago Museum Bulletin No. 1, Dunedin.

Forster, R.R., N.I. Platnick & J. Coddington. 1990. A proposal and review of the spider family Synotaxidae (Araneae, Araneoidea), with notes on theridiid interrelationships. Bulletin of the American Museum of Natural History 193:1–116.

Gertsch, W.J. 1979. American Spiders, 2nd edition. Van Nostrand Reinhold Co., New York.

Glatz, L. 1973. Der Spinnapparat der Orthognatha (Arachnida, Araneae). Zeitschrift für Morphologie der Tiere 75:1–50.

Griswold, C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). Smithsonian Contributions to Zoology 539:i–iii, 1–39.

Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zoological Journal of the Linnean Society 123:1–99.

Griswold, C.E., J.A. Coddington, N.I. Platnick & R.R. Forster. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). Journal of Arachnology 27:53–63.

Hajer, J. 1990. Snovací aparát pavouků rodu *Amaurobius* C.L. Koch, 1837 (Araneae: Amaurobiidae). Fauna Bohemiae Septentrionalis 14–15: 55–70.

Harvey, M.S. 1995. The systematics of the spider family Nicodamidae (Araneae: Amaurobioidea). Invertebrate Taxonomy 9:279–386.

Hebets, E.A., G.E. Stratton & G.L. Miller. 1996. Habitat and courtship behavior of the wolf spider *Schizocosa retrorsa* (Banks) (Araneae, Lycosidae). Journal of Arachnology 24:141–147.

Heimer, S. & W. Nentwig. 1991. Spinnen Mitteleuropas: ein Bestimmungsbuch. Verlag Paul Parey, Berlin.

Hormiga, G. 1994a. A revision and cladistic analysis of the spider family Pimoidae (Araneoidea: Araneae). Smithsonian Contributions to Zoology 549:i–iii, 1–104.

Hormiga, G. 1994b. Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae). Zoological Journal of the Linnean Society 111:1–71.

Hormiga, G. 2000. Higher level phylogenetics of erigonine spiders (Araneae, Linyphiidae, Erigoninae). Smithsonian Contributions to Zoology 609:i–iii, 1–160.

Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). Australian Journal of Zoology 43:313–364.

Kaihotsu, K. 1988. On the life history of *Cyspius orientalis* Yaginuma (Araneae: Pisauridae). Acta Arachnologica 37:13–22.

Karnovsky, M.J. 1965. A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. Journal of Cell Biology 27: 137A–138A (abstract).

Kaston, B.J. 1981. Spiders of Connecticut, revised edition (State Geological and Natural History Survey of Connecticut Bulletin 70). Department of Environmental Protection, Hartford.

Kokociński, W. 1968. Studia biometryczne nad wzrostem kądziołków przędnych w rozwoju postembrionalnym pająka *Agelena labyrinthica* (Clerck) (Araneae, Agelenidae). Studia Societatis Scientiarum Torunensis, Sectio E (Zoologia) 8: 253–334.

Kovoor, J. 1976. Caractères adaptatifs et caractères familiaux des glandes séricigènes dans le genre *Hippasa* E. Simon (Araneae, Lycosidae). Comptes Rendus de Troisième Réunion des Arachnologistes d'Expression Française, Les Eyzies 83–96.

Kovoor, J. 1977. La soie et les glandes séricigènes des arachnides. Année Biologique 16:97–171.

Kovoor, J. 1984. Anatomie, histologie et affinités de l'appareil séricigène des *Hersilia* Sav. et Aud. (Araneae: Hersiliidae). Canadian Journal of Zoology 62:97–106.

Kovoor, J. 1986. L'appareil séricigène dans les genres *Nephila* Leach et *Nephilengys* Koch: anatomie microscopique, histochimie, affinités avec d'autres Araneidae. Revue Arachnologique 7: 15–34.

Kovoor, J. 1987. Comparative structure and histochemistry of silk-producing organs in arachnids. Pp. 160–186. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Kovoor, J. & A. Muñoz-Cuevas. 1998. Structure and function of the silk-gland system in Oxyopidae (Araneae). Pp. 133–141. *In* Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. (P.A. Selden, ed.). British Arachnological Society, Burnham Beeches, Bucks.

Kovoor, J. & H.M. Peters. 1988. The spinning apparatus of *Polenecia producta* (Araneae, Uloboridae): structure and histochemistry. Zoomorphology 108:47–59.

Laemmli, U.K. 1970. Cleavage of structural proteins during the assembly of the head of bacteriophage T4. Nature 227:680–685.

Lawrence, R.F. 1964. A Conspectus of South African Spiders, Science Bulletin 369. South Africa Department of Agricultural Technical Services, Pretoria.

Lécaillon, M.A. 1905. Sur l'origine de l'habitude qu'ont les Lycosidae de porter leur cocon ovigère attaché aux filières. Comptes Rendus des Séances de la Société de Biologie et de Ses Filiales 59: 136–138.

Lizotte, R. & J.S. Rovner. 1989. Water-resistant sex pheromones in lycosid spiders from a tropical wet forest. Journal of Arachnology 17:122–125.

McCook, H.C. 1884. How *Lycosa* fabricates her round cocoon. Proceedings of the Academy of Natural Sciences of Philadelphia 36:138–139.

Mikulska, I. 1966. The spinning structures on the spinnerets (thelae) of *Nephila clavipes* (L.). Zoologica Poloniae 16:209–222.

Mikulska, I. 1969. Variability of the number of external spinning structures in female spiders *Clubiona phragmitis* C.L. Koch in populations to various degrees isolated. Zoologica Poloniae 19: 279–291.

Millot, J. 1935. Les glandes séricigènes des Salticides. Bulletin de la Société Zoologique de France 60:501–510.

Montgomery, T.H., Jr. 1903. Studies on the habits of spiders, particularly those of the mating period. Proceedings of the Academy of Natural Sciences of Philadelphia 55:59–149, plates IV–V.

Montgomery, T.H., Jr. 1909. Further studies on the activities of araneads, II. Proceedings of the Academy of Natural Sciences of Philadelphia 61: 548–569.

Müller, M.C. & W. Westheide. 1993. Comparative morphology of the sexually dimorphic orb-weaving spider *Argiope bruennichi* (Araneae: Araneidae). Memoirs of the Queensland Museum 33: 615–620.

Nation, J.L. 1983. A new method using hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. Stain Technology 58:347–351.

Nielsen, E. 1932. The Biology of Spiders, with Especial Reference to the Danish Fauna, Vol. I. Levin & Munksgaard, Copenhagen.

Palmer, J.M. 1990. Comparative morphology of the external silk production apparatus of "primitive" spiders. Doctoral thesis, Harvard University.

Peters, H.M. 1955. Über den Spinnapparat von *Nephila madagascariensis* (Radnetzspinnen, Fam. Argiopidae). Zeitschrift für Naturforschung 10b: 395–404.

Peters, H.M. 1982. Wie Spinnen der Familie Uloboridae ihre Beute einspinnen und verzehren. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 25:147–167.

Peters, H.M. 1983. Struktur und Herstellung der Fangfäden cribellater Spinnen (Arachnida: Araneae). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 26:241–253.

Peters, H.M. 1992. On the spinning apparatus and the structure of the capture threads of *Deinopis subrufus* (Araneae, Deinopidae). Zoomorphology 112:27–37.

Peters, H.M. 1993. Functional organization of the spinning apparatus of *Cyrtophora citricola* with regard to the evolution of the web (Araneae, Araneidae). Zoomorphology 113:153–163.

Peters, H.M. & J. Kovoor. 1989. Die Herstellung der Eierkokons bei der Spinne *Polenecia producta* (Simon, 1873) in Beziehung zu den Leistungen des Spinnapparates. Zoologische Jahrbücher: Abteilung für Allgemeine Zoologie und Physiologie der Tiere 93:125–144.

Peters, H.M. & J. Kovoor. 1991. The silk-producing system of *Linyphia triangularis* (Araneae, Linyphiidae) and some comparisons with Araneidae: structure, histochemistry and function. Zoomorphology 111:1–17.

Platnick, N.I. 1990. Spinneret morphology and the phylogeny of ground spiders (Araneae, Gnaphosoidea). American Museum Novitates 2978:1–42.

Platnick, N.I. 1999. A revision of the Appalachian spider genus *Liocranoides* (Araneae: Tengellidae). American Museum Novitates 3285:1–13.

Platnick, N.I. 2000. A relimitation and revision of the Australasian ground spider family Lamponidae (Araneae: Gnaphosoidea). Bulletin of the American Museum of Natural History 245:1–330.

Platnick, N.I. 2002. The World Spider Catalog, version 3.0. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog81–87/index.html.

Platnick, N.I., J.A. Coddington, R.R. Forster & C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016:1–73.

Platnick, N.I. & R.R. Forster. 1993. A revision of the New Caledonian spider genus *Bradystichus* (Araneae, Lycosidae). American Museum Novitates 3075:1–14.

Platnick, N.I. & M.U. Shadab. 1993. A review of the pirate spiders (Araneae, Mimetidae) of Chile. American Museum Novitates 3074:1–30.

Pötzsch, J. 1963. Von der Brutfürsorge heimischer Spinnen. Die neue Brehm-Bücherei, Heft 324. A. Ziemsen Verlag, Wittenberg.

Prentice, T.R. 2001. Distinguishing the females of *Trochosa terricola* and *Trochosa ruricola* (Araneae, Lycosidae) from populations in Illinois, USA. Journal of Arachnology 29:427–430.

Richter, C.J.J. 1970. Morphology and function of the spinning apparatus of the wolf spider *Pardosa amentata* (Cl.) (Araneae, Lycosidae). Zeitschrift für Morphologie der Tiere 68:37–68.

Richter, C.J.J., H.C.J. Stolting & L. Vlijm. 1971. Silk production in adult females of the wolf spider *Pardosa amentata* (Lycosidae, Araneae). Journal of Zoology, London 165:285–290.

Roberts, M.J. 1985. The Spiders of Great Britain and Ireland, Vol. 1, Atypidae to Theridiosomatidae. Harley Books, Great Horkesley, Colchester.

Roberts, M.J. 1995. Spiders of Britain and Northern Europe. HarperCollins Publishers, London.

Roth, V.D. 1993. Spider Genera of North America

with Keys to Families and Genera, and a Guide to Literature, 3rd ed. Available from J. Reiskind, Dept. of Zoology, University of Florida, Gainesville, FL 32611.

Scharff, N. & J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zoological Journal of the Linnean Society 120:355–434.

Scheffer, T.H. 1905. The cocooning habits of spiders. Kansas University Science Bulletin 3:85–114.

Schütt, K. 1995. *Drapetisca socialis* (Araneae: Linyphiidae): web reduction—ethological and morphological adaptations. European Journal of Entomology 92:553–563.

Schütt, K. 2000. The limits of the Araneoidea (Arachnida: Araneae). Australian Journal of Zoology 48:135–153.

Sekiguchi, K. 1955a. Differences in the spinning organs between male and female adult spiders. Science Reports of the Tokyo Kyoiku Daigaku, Section B 8:23–32.

Sekiguchi, K. 1955b. The spinning organs in subadult geometric spiders and their changes accompanying the last moulting. Science Reports of the Tokyo Kyoiku Daigaku, Section B 8:33–40.

Shear, W.A., J.M. Palmer, J.A. Coddington & P.M. Bonamo. 1989. A Devonian spinneret: early evidence of spiders and silk use. Science 246:479–481.

Sierwald, P. 1990a. Morphology and homologous features in the male palpal organ in Pisauridae and other spider families, with notes on the taxonomy of Pisauridae (Arachnida: Araneae). Nemouria, Occasional Papers of the Delaware Museum of Natural History 35:1–59.

Sierwald, P. 1990b. A systematic update of the family Pisauridae, or: are the Pisauridae a taxonomic goulash? American Arachnology 42:13 (abstract).

Sierwald, P. 1993. Revision of the spider genus *Paradossenus*, with notes on the family Trechaleidae and the subfamily Rhoicininae (Araneae: Lycosoidea). Revue Arachnologique 10:53–74.

Silva Davila, D. In press. Higher level relationships of the spider family Ctenidae (Araneae: Ctenoidea). Bulletin of the American Museum of Natural History.

Stratton, G.E. & G.W. Uetz. 1983. Communication via substratum-coupled stridulation and reproductive isolation in wolf spiders (Araneae: Lycosidae). Animal Behaviour 31:164–172.

Stubbs, D.G. 1991. Studies on the chemical composition, morphology, and production of the cocoon of the black and yellow garden spider *Argiope aurantia* (Lucas). M.S. thesis, University of New Hampshire.

Stubbs, D.G., E.K. Tillinghast, M.A. Townley & N.A. Cherim. 1992. Fibrous composite structure in a spider silk. Naturwissenschaften 79:231–234.

Tietjen, W.J. & J.S. Rovner. 1982. Chemical communication in lycosids and other spiders. Pp. 249–279. *In* Spider Communication: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Tillinghast, E.K. & M.A. Townley. 1994. Silk glands of araneid spiders: selected morphological and physiological aspects. Pp. 29–44. *In* Silk Polymers: Materials Science and Biotechnology (ACS Symposium Series 544). (D. Kaplan, W.W. Adams, B. Farmer & C. Viney, eds.). American Chemical Society, Washington, D.C.

Townley, M.A. 1993. Silk use during proecdysis in the spider *Araneus cavaticus* (Araneae, Araneidae). Doctoral dissertation, University of New Hampshire.

Townley, M.A., N.V. Horner, N.A. Cherim, C.R. Tugmon & E.K. Tillinghast. 1991. Selected aspects of spinning apparatus development in *Araneus cavaticus* (Araneae, Araneidae). Journal of Morphology 208:175–191, C5–C7.

Townley, M.A., E.K. Tillinghast & N.A. Cherim. 1993. Moult-related changes in ampullate silk gland morphology and usage in the araneid spider *Araneus cavaticus*. Philosophical Transactions of the Royal Society of London, Series B 340:25–38.

Wang, X.-P. 2000. A revision of the genus *Tamgrinia* (Araneae: Amaurobiidae), with notes on amaurobiid spinnerets, tracheae and trichobothria. Invertebrate Taxonomy 14:449–464.

Warburton, C. 1890. The spinning apparatus of geometric spiders. Quarterly Journal of Microscopical Science, New Series 31:29–39.

Wąsowska, S. 1967. The variability of the number of external spinning structures in female spiders of the genus *Tibellus* Simon (Thomisidae). Zoologica Poloniae 17:3–13.

Wąsowska, S. 1969. Particularités de l'appareil séricigène des mâles *Clubiona phragmitis* C.L. Koch. Zoologica Poloniae 19:505–515.

Wąsowska, S. 1977. Studies on the spinning apparatus in spiders. Postembryonic morphogeny of the spinning apparatus. Zoologica Poloniae 26: 355–407.

Wilson, R.S. 1969. Control of drag-line spinning in certain spiders. American Zoologist 9:103–111.

Wiśniewski, H. 1986a. Studies on the spinning apparatus of *Clubiona phragmitis* C.L. Koch (Araneida, Clubionidae). I. The external spinning apparatus. Zoologica Poloniae 33:71–81.

Wiśniewski, H. 1986b. Studies on the spinning apparatus of *Clubiona phragmitis* C.L. Koch (Araneida, Clubionidae). II. The structure of the internal spinning apparatus. Zoologica Poloniae 33:83–104.

Yaginuma, T. 1991. A new genus, *Shinobius*, of the Japanese pisaurid spider (Araneae: Pisauridae). Acta Arachnologica 40:1–6.

Yu, L. & J.A. Coddington. 1990. Ontogenetic changes in the spinning fields of *Nuctenea cornuta* and *Neoscona theisi* (Araneae, Araneidae). Journal of Arachnology 18:331–345.

Manuscript received 14 April 2002, revised 26 October 2002.

2003. The Journal of Arachnology 31:246–273

WHEN TO QUIT? ESTIMATING SPIDER SPECIES RICHNESS IN A NORTHERN EUROPEAN DECIDUOUS FOREST

Nikolaj Scharff[1], Jonathan A. Coddington[2], Charles E. Griswold[3], Gustavo Hormiga[4] and **Per de Place Bjørn[1]**: [1]Dept. Entomology, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark; [2]Dept. Systematic Biology, National Museum of Natural History NHB 105, Smithsonian Institution, Washington DC, 20013-7012, USA; [3]Dept. Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, USA; [4]Dept. Biology, George Washington University, Washington DC, 20052, USA; To whom correspondence should be addressed: Nikolaj Scharff (+45 35321107, fax +45 35321010; E-mail: nscharff@zmuc.ku.dk

ABSTRACT. Terrestrial arthropod surveys and inventories frequently suffer from undersampling bias; common species are over-represented and rare species may be missed entirely. This study compared a rapid (3 days) and intense inventory of spiders from one hectare of a mature beech forest (*Fagus sylvaticus*) in Hestehaven, Denmark, comprising 8,710 adult spiders of 66 species to a previous, much more thorough, bi-weekly survey of two years duration from the same site that comprised 42,273 spiders (adult and juvenile) of 141 species. Non-parametric species richness estimators were used to assess the degree of undersampling bias in various data partitions. The current study used five experienced, four novice collectors, and five semi-quantitative collecting methods. Method and time of day strongly affected numbers of species and adults per sample. Collector experience affected numbers of species but not numbers of adults per sample. Despite the intensive collecting, number of adults per sample did not decrease over the course of the study. At the end of the sampling, 31 species were still rare in the sample (singletons or doubletons). Non-parametric richness estimators suggest that the actual richness of adult spiders in the study plot at this time of year and susceptible to the methods used was about 80 species. Species turnover between the two surveys (ca 23 years) was remarkably small: the two lists were 92% identical. The baseline study suggests that the rarity of 12 of the 31 rare species was artifactual (10 due to phenology, one to method, another to spatial edge effects). The rarity of the remainder is unexplained and by default is interpreted as undersampling bias.

Keywords: Biodiversity, Araneae, inventory, species richness estimation, singletons, beech forest, Denmark

Conservation and natural resource management decisions notoriously draw mainly on ecological information obtained from vertebrates and plants (Kremen et al. 1993; Prendergast et al. 1993). Environmental monitoring is much the same, even though it is widely recognized that patterns in vertebrates and plants do not exemplify the patterns in many other groups in the same habitat (Groombridge 1992; Stork & Samways 1995). The bias towards vertebrates and woody plants stems from a simple reason: surveys are usually so short and resource-limited that only the best-known and least diverse groups can be adequately sampled.

One consequence is that arthropods, the most diverse organisms in any terrestrial environment (May 1978), often go unstudied (Longino 1994). The most basic data provided by traditional biodiversity assessments is the richness and relative abundance of species in a given area (May 1975; Taylor 1978) and on both counts arthropods present formidable challenges (Erwin 1983; McKamey 1999; Novotny & Basset 2000). Arthropods, however, may provide information not otherwise obtainable from traditional focal groups; information that may turn out to be crucial for long term management of existing natural resources (Kremen et al. 1993). They are small in size (therefore abundant), short-lived (going through many generations within short time spans), diverse and often have limited distributions and strict environmental requirements

(e.g., many mites and small spiders live exclusively within a few square meters of soil on the forest floor). In theory, they should map environmental diversity and track environmental changes more quickly and precisely than longer-lived, more flexible organisms such as vertebrates and plants.

Collecting prodigious numbers of species and individuals is easy, but the proportion of the total available fauna represented in such collections is usually unknown. The omnipresent high frequency of rare species instead suggests that arthropod communities in general are drastically under-sampled by conventional survey efforts, even large ones. To judge the real utility of arthropods for environmental assessment and monitoring, therefore, we first need to be able to assess the thoroughness and efficiency of inventories and censuses themselves. These, in turn, require relatively fast, cheap, efficient and robust sampling protocols. Such methods have been proposed for spiders in tropical ecosystems by Coddington and co-workers (Coddington et al. 1991) and tested in Cameroon, Tanzania (Sørensen et al. 2002), Madagascar, Bolivia (Coddington et al. 1991, 1996), Guyana, Tobago, southern USA (Coddington et al. 1996; Dobyns 1997), Slovenia (Kuntner & Baxter 1997), Denmark (this study) and Greenland (Larsen & Rasmussen 1999).

The optimal test of empirical and analytical inventory methods would be against a "known universe" in which the fauna is a) natural, b) diverse, and c) thoroughly known. For spiders such sites are few indeed. One possibility is the International Biological Project (IBP) site (Thamdrup et al. 1975) in Hestehaven, Denmark. The information available on spiders from this mature beech forest is unique because collecting was carried out biweekly for several years in the 1970's with a large battery of ecological sampling methods. All material collected was identified to species and instar, including juveniles (Toft 1976). The accuracy of juvenile identifications is frequently, and perhaps justifiably, questioned. Toft (1976) argued that in his specific case the error rate was acceptably low because the somatic morphology of many species was distinct, the total diversity was low and the clarity of distinct phenologies resulting in unambiguous adults made retroactive identification of juveniles feasible (see also Toft 1983). Because even crude measures of the effect of ignoring juveniles are almost nonexistent in the literature (but see Norris 1999) and because the question is intrinsically interesting, for the purposes of comparison to our data we accept the accuracy of Toft's determinations. Data from identified juveniles reveal community phenology patterns, and also can quantify the bias resulting from the practical necessity of modern inventories to focus on adult animals only, whether in tropical inventories or less well understood temperate areas. The proportion of juveniles in a tropical sample seems remarkably constant at 60–70% (Coddington, Scharff, pers. obs; Russell-Smith & Stork 1995; Silva 1996). Tropical assessments to date have worked with adults only, because tropical spider faunas are so little known that identification of juveniles of other than ostentatious species is impossible. Even adults are often impossible to identify to anything but morphospecies in the tropics. The main objective of this study was to evaluate in several ways this inventory design against a "known spider universe." Of course, local faunas do change with time (in this case a 23 year hiatus) and stochastically due to dispersal and local extinctions. Nevertheless, we know of no spider communities from climax communities as well known as that of Hestehaven. We wanted to test how well the method worked in a temperate forest community where a few species would be numerically dominant and wished to investigate the impact of extremely rapid surveys using many simultaneous collectors (with a mix of professional arachnologists and collectors with little or no collecting experience) on the fauna, and to learn how unavoidable factors such as method, day vs. night collecting and collector experience affected results. Finally we wished to calibrate richness statistics from an extremely rapid and intense inventory against the known richness for the same season and against the total known annual spider fauna.

METHODS

Study site.—The study was carried out during 3 days, August 29–September 1, 1994, in the mixed coastal forest, Hestehaven (176 hectares), about 25 km NNE of Århus, Eastern Jutland, Denmark. The forest is approximately 15 meters above sea level and surrounded by agricultural land. A one hectare sampling plot

(56°17.46′N, 10°28.50′E) was established within a 3-hectare climax stand of mature beech (*Fagus silvaticus* L.). A map of the forest including the location of the sampling plot and the distribution of vegetation is given in Rasmussen et al. (1982; fig. 2). The nearest stand of non-beech vegetation is located approximately 75 meters from the sampling plot and consists of spruce. The distance from the sampling plot to the nearest agricultural area is 250 meters. The plot perimeter was marked with strings to ensure that all collecting only took place within the plot. Danish ecologists have intensively studied the arthropod fauna of this particular stand of beech in the period 1969 to 1972 in connection with an international study of beech-wood ecosystems (Nielsen 1974a, 1974b, 1974c, 1975, 1977, 1978a, 1978b, 1987). The composition of the spider fauna was analyzed by Toft (1976, 1978) and other scientific results of this beech-wood project in Hestehaven have been published in 66 scientific papers. There is no other place in Denmark, and few elsewhere in the world, where a well-known arthropod fauna has been studied in such detail.

The oldest beech trees within the plot are more than 110 years old and very little regeneration occurs. The density of beech trees is approximately 190 trees per hectare. Mature beech forests severely reduce light reaching the forest floor, and their root systems effectively compete against other woody plants. The Hestehaven forest floor vegetation is dominated by *Anemone nemorosa* L., *Melica uniflora* Retz., *Asperula odorata* L., *Hordeum europaeum* (L.), *Circaea lutetiana* L., *Carex sylvatica* Huds., *Veronica montana* L., and *Ficaria verna* Huds., (Nielsen 1977). At the end of August, the forest floor was dominated by knee-high grass and scattered areas with ferns. As is typical for mature northern European beech forests, the understory supported few bushes and small trees and therefore very little vegetation that could be reached by hand.

Collectors.—Nine collectors worked simultaneously in the field. Five of these were classified *a priori* as "experienced" (many years collecting spiders), and the other four as inexperienced (no or less than one year experience in spider collecting). Sampling began on August 29 at night (2000–2400), continued day (0900–1800) and night on August 30–31, and concluded during the morning of September 1. Even by "rapid" inventory standards three days is extremely short, but various scheduling conflicts prohibited a longer duration. Collecting both night and day is important to make sure that both diurnal and nocturnal species are collected. Each collector was asked to use each collecting method a certain number of times during the fieldwork. Collectors were limited to 6 or fewer samples per day or night to avoid fatigue. One person kept track of all the samples taken by various collectors, methods and times of day, thereby ensuring that the different methods were used both day and night and making sure that work was carried out efficiently.

Collecting methods.—We used five collecting methods to access the spider fauna within the plot. These were chosen to access as many different habitats, and to overlap as little as possible. Because the time span of the inventory was so short we did not use pitfalls and for logistic reasons Berlese or Tullgren funnel extraction of litter were not feasible. Each sample represented one method applied for 1 hour of active, continuous collecting (i.e., including time required to transfer the catch to a vial, but excluding time due to interruptions). Collectors used countdown time functions in wristwatches to time themselves. The countdown was suspended if the collector moved to a new habitat patch or if occupied with non-collecting tasks (i.e., logistics, equipment maintenance, field notes, photography, etc.). A sample therefore usually took somewhat more than one hour to finish.

Aerial: Searching through the vegetation from knee height to as high as the collector can reach above his/her head. Toti et al. (2000) changed the name to "aerial" to emphasize the target guild, but it is synonymous with "looking up" method of Coddington et al. (1991).

Ground: Searching the ground and lower vegetation below knee height. Toti et al. (2000) changed the name to "ground" to emphasize the target guild, but it is synonymous with "looking down" method of Coddington et al. (1991). The collector searches on hands and knees for spiders on the surface of plants, tree stems, logs, rocks, and the ground surface but not the interior of leaf litter, logs, under stones etc.

Sweeping: Searching the lower herb layer with a sweep net (net diameter 36 cm). The

net was emptied after a few sweeps to avoid damage to the specimens. In this study the diversity of the vegetation available for sweeping was rather limited and dominated by grass and small, scattered areas with ferns.

Beating: Sharply tapping branches or other vegetation with a stout stick while holding a 0.6 m^2 beating tray underneath to catch the falling spiders. Beating tray areas varied among collectors, but because samples were defined on the basis of time rather than repetitions or area, beating tray areas are probably unimportant. Small spiders are efficiently transferred from the beating tray to the sample vial with an aspirator or pooter. Because mature beech trees have very few lower branches, this plot had little vegetation suitable for beating, and consequently we allocated fewer resources to beating and more resources to other methods. Beating at night was difficult because of headlamp glare and yielded sparse results, so we eliminated that combination.

Cryptic: Searching for adult spiders under logs, inside rotten logs, sifting litter, manual search within leaf litter, under rocks, inside holes, under bark, etc. It is intended to access any habitat the "cryptic" fauna is likely to occupy and allows the collector to use the method best suited to the opportunities the particular habitat offers.

Specimens and sorting procedures.—Each sample was labeled with locality, date, collector, method, and replicate number (if two samples were otherwise identical). Samples were more or less immediately transferred to 70% ethanol in a WhirlPak® bag so that field vials could be reused. A mixture of experienced and inexperienced (students) arachnologists working in groups sorted the collection to species so that the experienced arachnologists could validate identifications (identifiers are listed in the Acknowledgments). All identifications of singletons and doubletons were checked and verified by several arachnologists. Voucher specimens of each species identified in this study are deposited at the Zoological Museum, University of Copenhagen (ZMUC). Duplicates have been deposited at the Smithsonian Institution, Washington D.C. (USNM) and at the California Academy of Sciences (CAS), San Francisco, CA.

Statistical analysis.—Statistical analyses and graphs were produced with Systat 9.0 (SPSS Inc. 1999). To analyze the effects of inventory design parameters on results, we chose analysis of variance in which method, time of day, and collector experience were treated as independent factors, and numbers of adults and species per sample, respectively, as dependent variables. Post-hoc Tukey HSD tests were used to determine which treatments were responsible for significantly different factors. Due to the large number of factors and treatments, some ANOVA cells were empty. For example, we did not beat at night, and therefore beating was excluded from analyses involving method and time of day. A third analysis investigated the influence of individual collectors on the overall mean number of species per sample. A fourth analysis contrasted the number of species per sample by method and time of day for sets of experienced and inexperienced collectors. Species accumulation curves and richness estimates were produced with EstimateS 6.0b1 (Colwell 2000). The current dataset is hereafter referred to as "ZMUC" (Zoological Museum University of Copenhagen) and the historical dataset from Toft (1976) is referred to as "AAU" (Aarhus University).

Lognormal distributions were computed manually as no available programs retain the benefits of the classical approach and also solve the problem of the biased 0–1 octave (Lobo & Favila 1999; Longino et al. 2002). Many programs define abundance classes as log base 3, which prevents integer values from falling on class boundaries, but it also collapses the full distribution to relatively few abundance classes for most datasets, and the chi square test therefore lacks power. Log base 2, as Preston (1948) originally suggested, maintains a relatively fine-grained classification of the data and is easy to compute. The problem of singleton species is more subtle. Most techniques (e.g. Preston 1948, 1962; Ludwig & Reynolds 1988; see also Bliss 1966) apparently divide the singleton species between the 0.5–1 and 1–2 octave, just as other values falling on class boundaries are divided. However, all higher octaves potentially receive from both neighboring boundaries, but the 0.5–1 octave cannot draw from the 0.25–0.5 octave, as species with fractional relative abundances are not observed. The practical effect of this bias is that the 1–2 octave is always larger than the 0.5–1 octave because it

contains half the 1's and 2's. This produces a false mode in the data and distorts the calculation of the lognormal parameters. Because the 0.5–1 octave is always biased, it should be ignored during the calculation of parameters. We iteratively assigned "octave" numbers (r) to the log base 2 abundance classes and estimated the lognormal parameters S0 (mode) and a (width) using the Nonlin module of Systat 5.2, with Quasi-Newton estimation and least squares fit (model: $S = S_0 e^{(-a2 \cdot r2)}$. The optimal set of assignments minimized the chi square difference between estimated and observed richness (s) across octaves.

"Sampling intensity" is the ratio of specimens to species (Coddington et al. 1996; Sørensen et al. 2002). The chief virtue of this measure is its simplicity: it can be calculated for any inventory whatever. Given roughly comparable relative abundance distributions and richness, it crudely compares sampling effort to the size of the universe being sampled (but see Gotelli & Colwell (2001) for pitfalls). Inventory completion (or completeness) is the extent to which an inventory, or inventory component, samples the faunal partition available to it (Sørensen et al. 2002). Equal sampling effort in microhabitats or diversity partitions that vary in richness can result in disproportionately rich microhabitats being disproportionately undersampled. The usual symptom of such biased sampling is a strong correlation between sampling effort and richness (Heyer et al. 1999), which in turn can bias conclusions about relative species richness. For spiders, different methods and day versus night collecting access different partitions of the overall community with varying efficiency, and those partitions also differ in richness and abundance (Silva 1996; Silva & Coddington 1996; Coddington et al. 1996; Sørensen et al. 2002). We measure "inventory completion" in an inventory partition as the ratio of observed richness to the Chao1 richness estimate for that partition (Sørensen et al. 2002). Comparison of species richness estimators generally favor Chao2 as among the least biased, most efficient, and most robust methods (Colwell & Coddington 1994; Peterson & Slade 1998; Walter & Martin 2001). Chao2, however, requires replicate sampling. Chao1 performed nearly as well as Chao2 in tests, is simply calculated from tabular data, and is the only non-parametric richness estimator that does not require replicate sampling. It can therefore be applied to more kinds and qualities of inventory data, and will enable broader comparison of completion statistics across inventories. Our allocation of sampling effort reflected the idiosyncrasies of the site and our *a priori* assessment of the relative richness of different microhabitats. The dense beech canopy had suppressed nearly all understory shrubs and the beech trees themselves lacked all lower branches. The herb layer was knee-high uniform grass with interspersed fern clones. Therefore, we allocated relatively less effort to beating and more to cryptic and ground searching compared to aerial searching and sweeping. Ideally, an inventory should be an unbiased sample of the community. In practical terms this means that each method or time of day partition should reach the same degree of inventory completion; equivalently, the coefficient of variation of inventory completion should be equal to or less than that of sampling effort investment across the variation inventory partitions.

RESULTS

The nine collectors produced 149 samples over 3 days containing a total of 8,710 adults of 66 species from the one hectare plot (Appendix; Table 1). The mean number and standard deviation of total samples per collector was 16.56 ± 0.72 (n = 149), aerial was 2.33 ± 0.71 (n = 21), beating was 0.89 ± 0.71 (n = 8), cryptic was 5.56 ± 1.59 (n = 50), ground was 5.22 ± 1.72 (n = 47) and sweeping was 2.56 ± 1.01 (n = 23). Overall sample intensity (specimens : species) was 132, but it ranged from 24–110 per method (because methods often catch the same species, the total sample intensity is usually greater than that of any partition). The figure of 132 may seem high, but is biased by the extraordinary abundance of two species (*Linyphia triangularis* (Clerck 1757) and *Drapetisca socialis* (Sundevall 1833)). If these are excluded, the ZMUC sampling intensity falls to the mediocre value of 12, which is well below 30, our current working guess of the minimum sampling intensity statistic typically sufficient to yield convincingly asymptotic richness estimates. Nineteen species were singletons and 12 were doubletons. Despite the large number of animals collected, the final percentage of singletons was high at 29%. *Linyphia trian-*

Table 1.—Summary values for the ZMUC inventory at Hestehaven. SD = Standard deviation, Spp = Species. Percent method bias is the deviation of the method's inventory completion statistic from the grand mean among methods. Percent effort investment is the percent of total samples invested in a particular method.

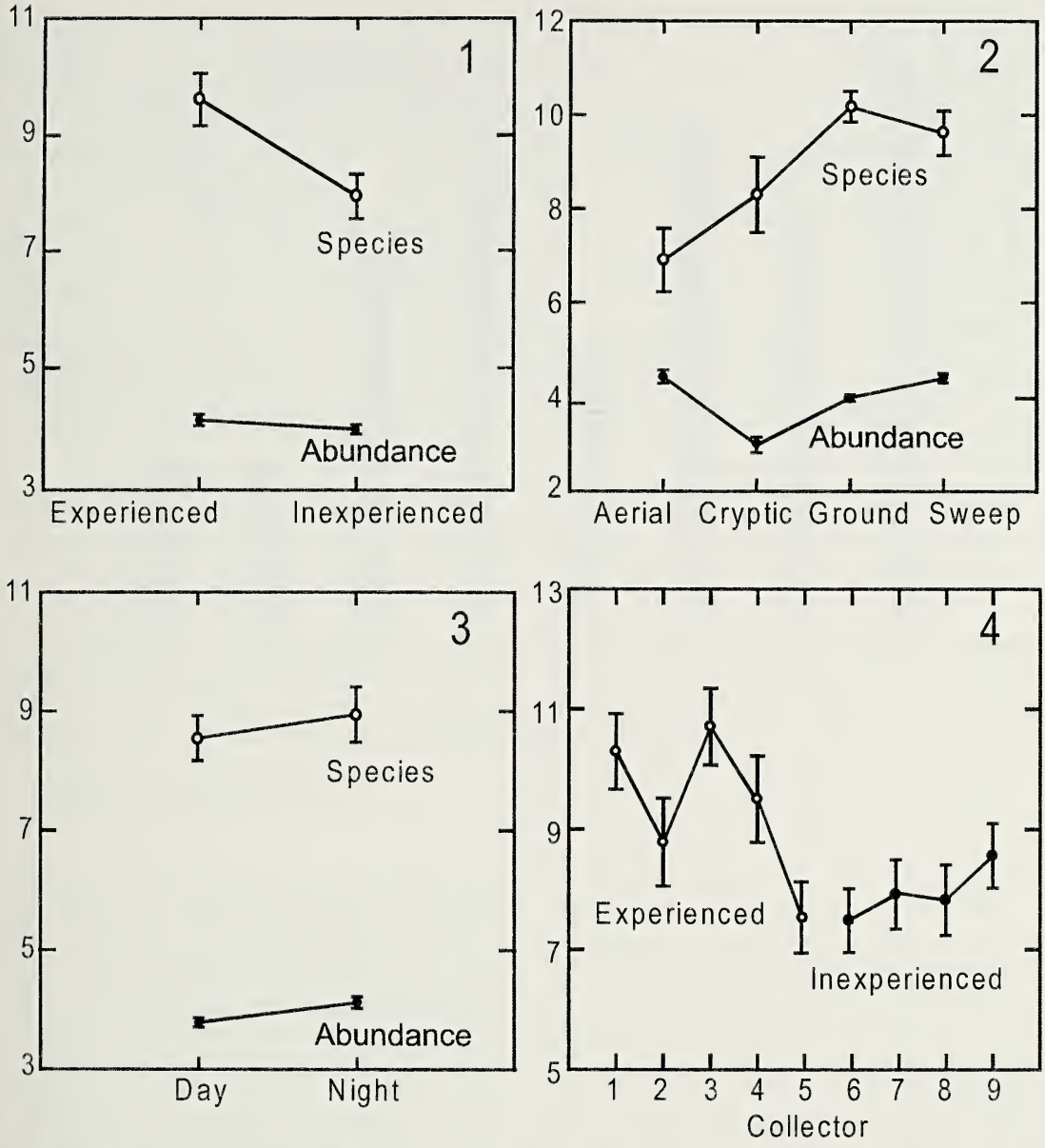
	Collection methods				Time			
	Aerial	Beating	Sweeping	Ground	Cryptic	Day	Night	Total
No. of samples	21	8	23	47	50	96	53	149
Mean no. of ind./sample	120	51	92	58	19	41	90	58
SD ind./sample	72	29	44	17	9	34	9	49
Mean no. of spp./sample	7	7	10	10	8	9	9	9
SD spp./sample	2	2	2	2	3	3	3	3
Total no. of individuals	2,526	405	2,126	2,713	940	3,960	4,750	8,710
Total no. of species	23	17	30	38	34	53	44	66
Sample intensity	110	24	71	71	28	75	108	132
No. of unique species	2	1	9	9	9	22	13	30
Singletons	5	5	10	13	7	17	13	19
Doubletons	4	0	2	3	4	7	5	12
% Singletons	22	29	33	34	21	32	30	29
Chao1 estimate	26 ± 3	25 ± 8	55 ± 16	66 ± 16	40 ± 5	74 ± 13	61 ± 13	81 ± 7
% Inventory Completion	88	68	55	58	85	72	72	81
% Method Bias	17	−3	−16	−13	14	1	1	10
% Effort Investment	14	5	15	3	34	64	36	100

gularis and *D. socialis* at 2,135 and 2,046 individuals, respectively, dwarfed the abundances of other species and accounted for 48% of the total inventory. The true relative abundance of at least *D. socialis* was even greater because we truncated collection of this species at 10 specimens per sample after the first night. We continued to collect *L. triangularis* because it could not be reliably distinguished in the field from the much rarer *Linyphia hortensis* Sundevall 1830 or *Neriene clathrata* (Sundevall 1830). Hourly samples averaged 58 individuals and 9 species overall. Cryptic sampling yielded the fewest individuals per hour (19) and aerial the most (120), but methods were remarkably uniform in average numbers of species per sample (7–10). Richness per sample ranged from 2–14 species, and abundance from 2–273 individuals.

Collector experience, method, and time of day.—Abundance but not number of species per sample required log-transformation prior to analysis to maintain normality. Collector experience, method, and time of day were treated as independent factors in the ANOVA model, and numbers of adults and species per sample, respectively, as dependent variables. As mentioned under "Methods," beating at night is difficult due to glare and at this site was unproductive. We therefore excluded beating at night as a method-time of day combination and excluded it from these analyses. Collector experience significantly increased number of species per sample, but not number of adults ($F = 7.029$, $P < 0.000$, Fig. 1). Method affected both number of species ($F = 7.029$, $P < 0.000$) and numbers of adults per sample ($F = 20.429$, $P < 0.000$, Fig. 2). Aerial and sweep sampling produced more adults per sample than cryptic ($P < 0.000$ vs aerial; $P < 0.000$ vs. sweeping) or ground sampling ($P < 0.026$ vs aerial; $P < 0.003$ vs. sweeping), and cryptic and ground also differed significantly from each other ($P < 0.000$). For numbers of species per sample, sweeping, ground and cryptic collecting did not differ from each other (Fig. 2), but aerial produced fewer species per sample than ground ($P < 0.000$) or sweeping ($P < 0.006$). Night collecting significantly increased numbers of adults per sample ($P < 0.009$) but not species (Fig. 3). The model explained 75% of the variance in numbers of adults and 34% of the variance in numbers of species per sample. No factor interactions were significant in either ANOVA. To investigate more fully the effect of individual collectors on numbers of species per sample, we ran an ANOVA with collector identity and method as independent factors and numbers of species per sample as the dependent variable (Fig. 4). A post-hoc Tukey HSD test showed that collectors 5 and 6 differed from 1 and 3, and collectors 7 and 8 also differed from 3. Collector 5, classified a priori as experienced was more similar to inexperienced collectors (collector 5, Fig. 4). During the day experienced collectors were much more efficient at aerial searching and beating, less so at cryptic and ground searching, and indistinguishable from inexperienced collectors at sweeping (Fig. 5). At night inexperienced collectors were only slightly less efficient at aerial sampling and were equivalent sweepers, but the gap widened during cryptic and ground collecting (Fig. 6). Sweeping was the only method used here that seemed completely unaffected by experience. In summary, method strongly affected both abundance and richness, experience produced moderately larger numbers of species but not individuals and spiders were generally more accessible (active) at night than during the day.

Complementarity of methods.—Thirty species were unique to single methods and the overlap between methods was moderate, ranging from 11 species shared between "ground" and "beating" to 22 species shared between cryptic and ground. Each method sampled unique species not found by the other methods (Table 1).

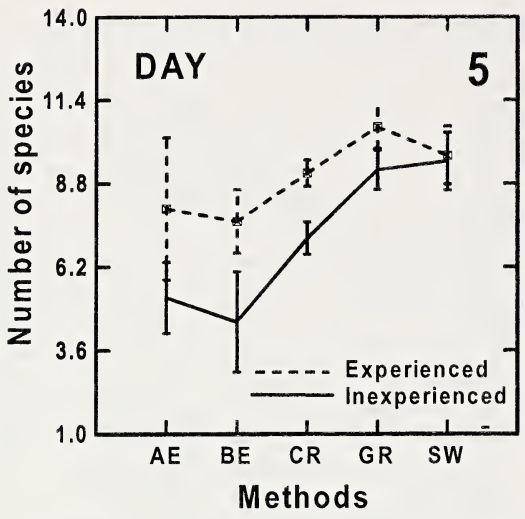
Faunal depletion.—We tested for the effect of intensive collecting on the overall spider fauna by plotting individuals per sample against chronologically arranged sample number (Fig. 7). If all species are included, abundance does decrease over the sampling period ("All species," Fig. 7). However, this decrease is primarily due to our decision after the first night to truncate collection of the very abundant *D. socialis* in each sample after 10 animals had been collected. If the two most common species are excluded (*D. socialis*, *L. triangularis*), spider abundance per sample did not decrease significantly over the course of the study ("most common excluded," Fig. 7). We further checked this result by lagging the data and testing for cross-correlation to the

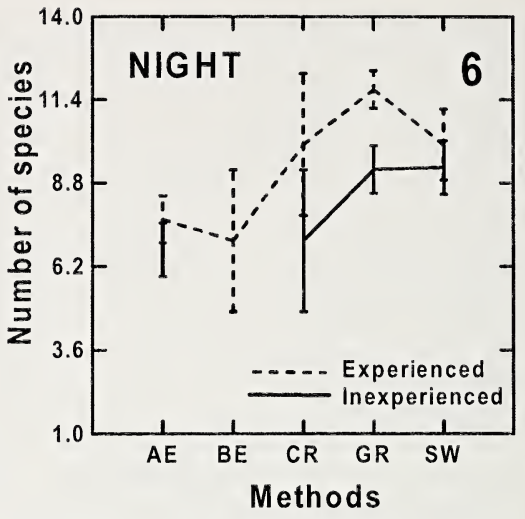


Figures 1–4.—Least squares means and standard errors from analysis of variance on number of species (open circles) and log of numbers of adults (closed circles) per: 1. Sample by collector experience. Experience increases richness but not abundance per sample; 2. Sample by method. For abundance, cryptic and ground sampling differ from each other and both from aerial and sweeping. For richness, aerial differs from ground and sweeping; 3. Sample by time of day. Night collecting increases number of adults but not species; 4. Least squares means and standard errors from analysis of variance on number of species per sample by experienced (open circles) and inexperienced (closed circles) collectors.

original time line; the plot showed no significant trend. Collector fatigue and boredom with common species probably also played a role.

Inventory completion.—The mean inventory completion by method was 71%, and separate methods deviated −16% to +17% around this value (percent method bias, Table 1). Figure 8 compares observed to estimated richness for each method, day versus night, and the total inventory. Aerial sampling was most complete at 88% and sweeping least





Figures 5–6.—Least squares means and standard errors from analysis of variance on number of species per sample by method and collector experience during: 5. Day; 6. Night (Abbreviations: AE = Aerial, BE = Beating, CR = Cryptic, GR = Ground, SW = Sweeping).

complete at 55% despite essentially equal sampling effort. Day and night sampling, on the other hand, were equally complete at 72%, despite nearly twice as much investment in daytime sampling (Table 1). Overall, the coefficient of variation for sampling effort across methods and times of day was 68%, but that for inventory completion only 18%, showing

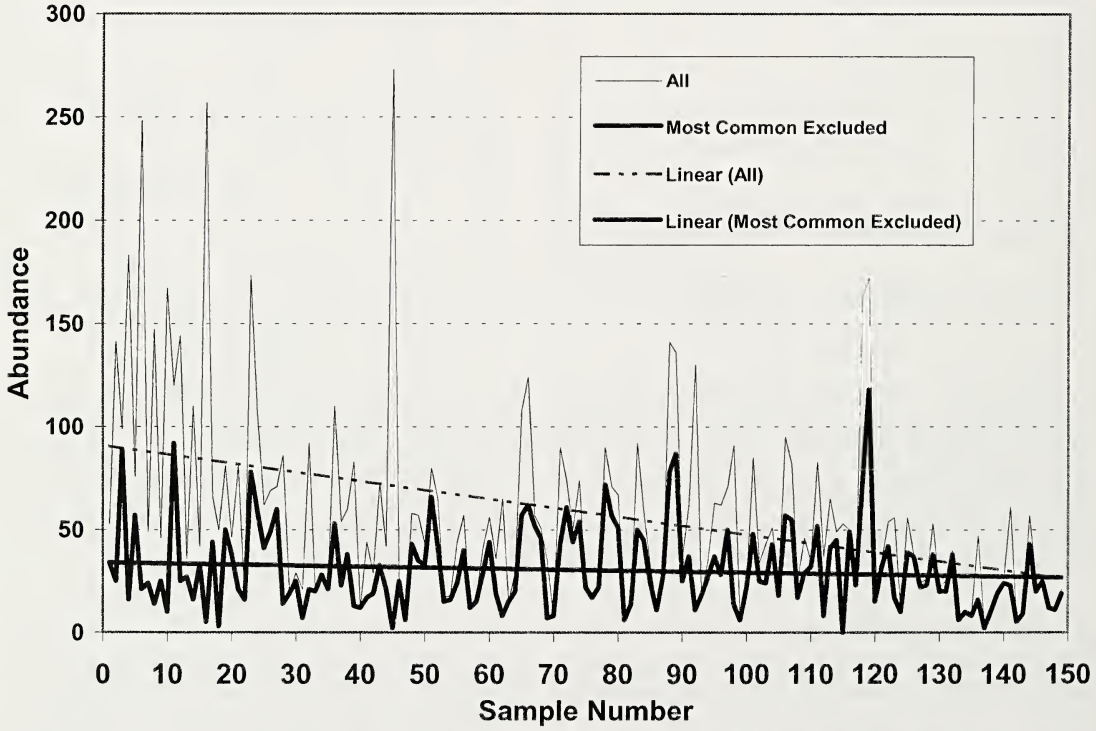


Figure 7.—Number of adults per chronologically arranged sample for all the data and with the two most common species removed, with least squares linear fits to each sequence.

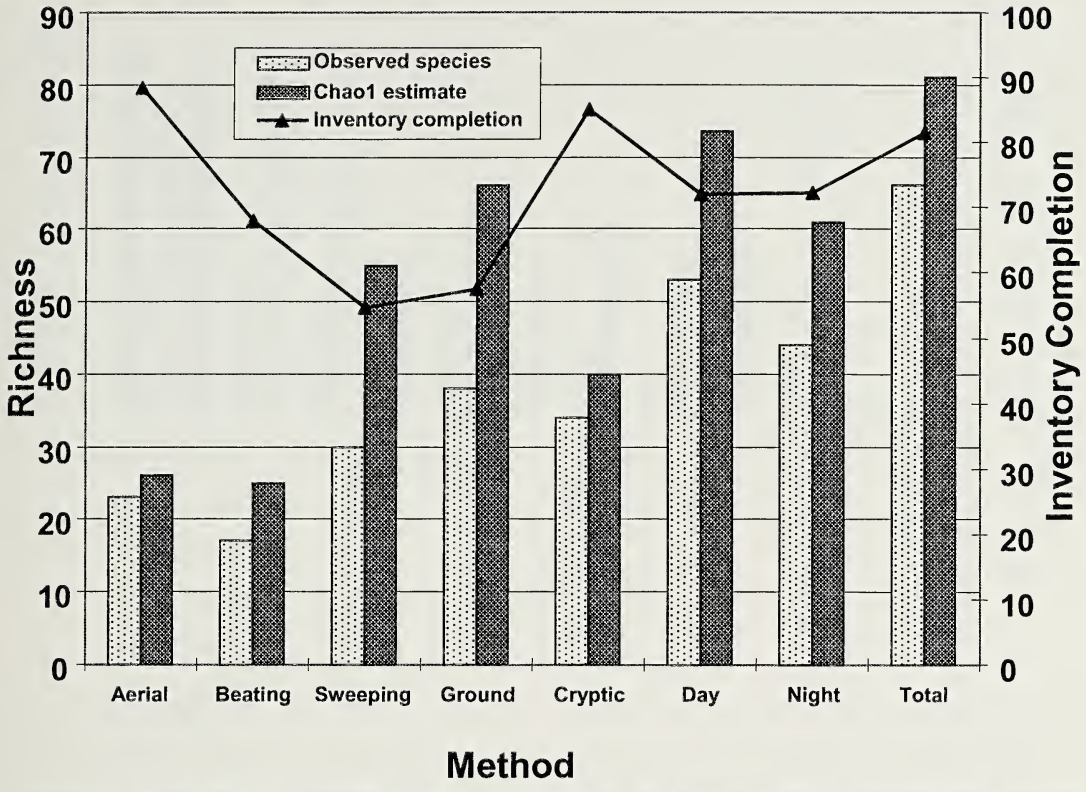


Figure 8.—Total species caught by each method and time of day, with Chao1 estimates and inventory completion values for each partition.

that differential investment does compensate for differential richness in habitats. Nevertheless, sweeping and ground faunas appear to have been relatively undersampled and aerial and cryptic faunas relatively oversampled compared to the mean inventory completion, so that this particular allocation profile mitigated, but did not eliminate bias due to differential return on effort by method. Richness plotted against individuals collected still shows positive slope and correlation (Fig. 9, "original"). If "return on effort" were saturated, the regression line would be essentially flat. Although the current inventory still shows a non-zero slope and correlation, less effort would have yielded an even steeper slope. Figure 9 also plots regressions for one third and two thirds of all samples randomly chosen from each method. One third as much effort shows a much steeper slope, and two thirds is intermediate between one third and the total data set, as expected (Fig. 9). Although substantial effort was invested in this inventory, it was nevertheless insufficient to eliminate correlation between sampling effort and observed richness.

Richness estimation.—The rank-abundance plot for the 66 observed species shows a characteristically temperate faunal distribution with relatively many common and few rare species compared to tropical faunas (Fig. 10). The ZMUC data fit a lognormal distribution (chi square goodness of fit, $P < 0.7$) but show no mode (Fig. 11, "ZMUC"). The richness estimation curves show typical signs of an incomplete inventory (Fig. 12): the observed curve terminates substantially below the estimator curves and is not asymptotic, the estimators are not consistently asymptotic, the uniques curve is still rising or barely flat, lies relatively far above the doubletons curve, and shows no sign of crossing it, and the doubletons curve is definitely still rising. At face value, the richness estimators presented here imply about 80–90 species present as adults in the area sampled and accessible to the methods used, of which we observed only 66 (73%).

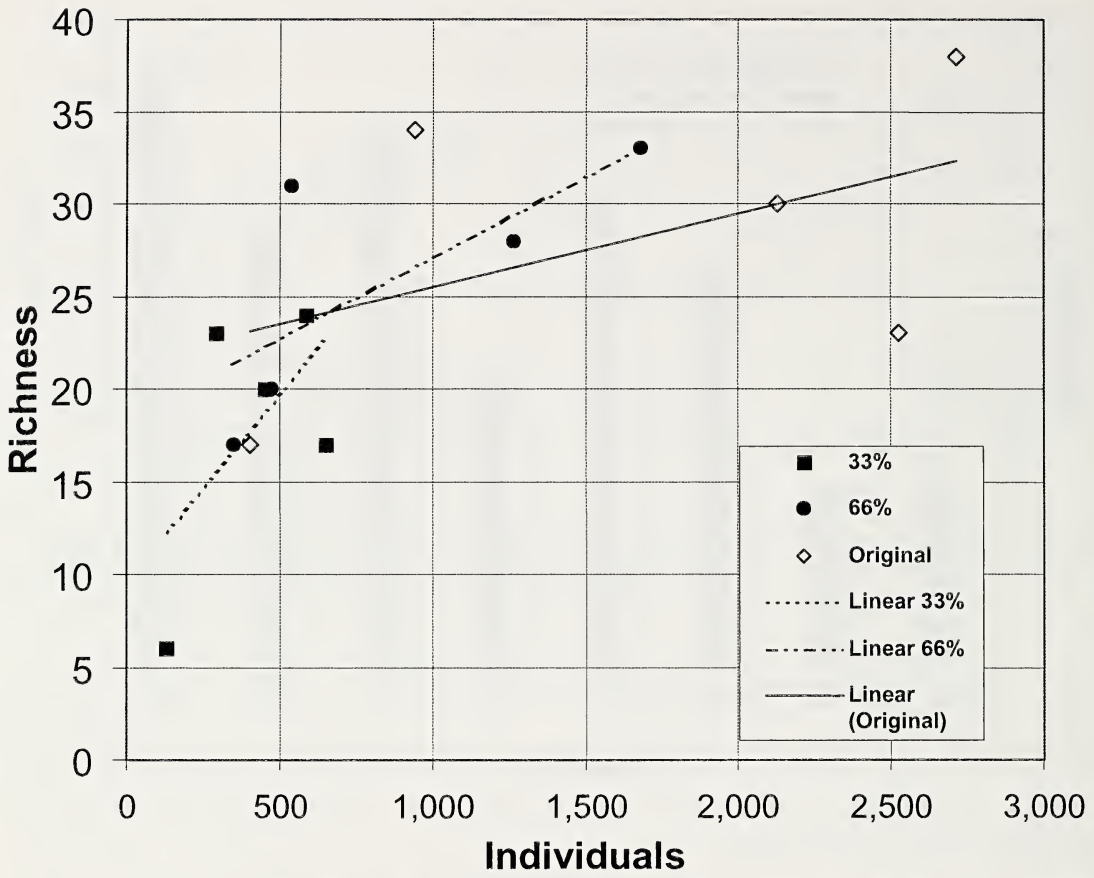


Figure 9.—The correlation between richness and sampling effort by method (measured as number of individuals sampled) for 33%, 66% and the total (original) dataset, with least squares fits to each partition.

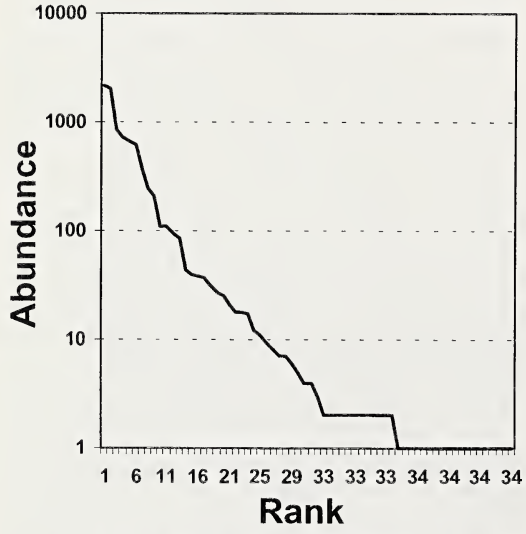


Figure 10.—Rank abundance diagram for the total dataset.

Comparison to AAU study.—Søren Toft sampled the same hectare as well as the surrounding beech forest on a roughly biweekly schedule from July 1969–July 1971 using five methods: litter extraction, pitfall and stem traps, sweeping and "clubs": a method in which trees are struck with very large clubs to dislodge the canopy fauna (Nielsen 1975; Toft 1976). He obtained 43,580 spiders of 147 species (plus 3 species that he could only assign to genus) over the two year study and classified them all to species and, if juvenile, to instar. The original AAU data sheets still exist and we used them to compile a database of species by instar, abundance and sample characteristics (i.e. date, method, etc.). Not surprisingly after 23 years, some discrepancies could not be resolved, but the database eventually accounted for 42,273 animals of 141 species, comprising 15,533 adults and 26,740 juveniles (Table 2). The missing spe-

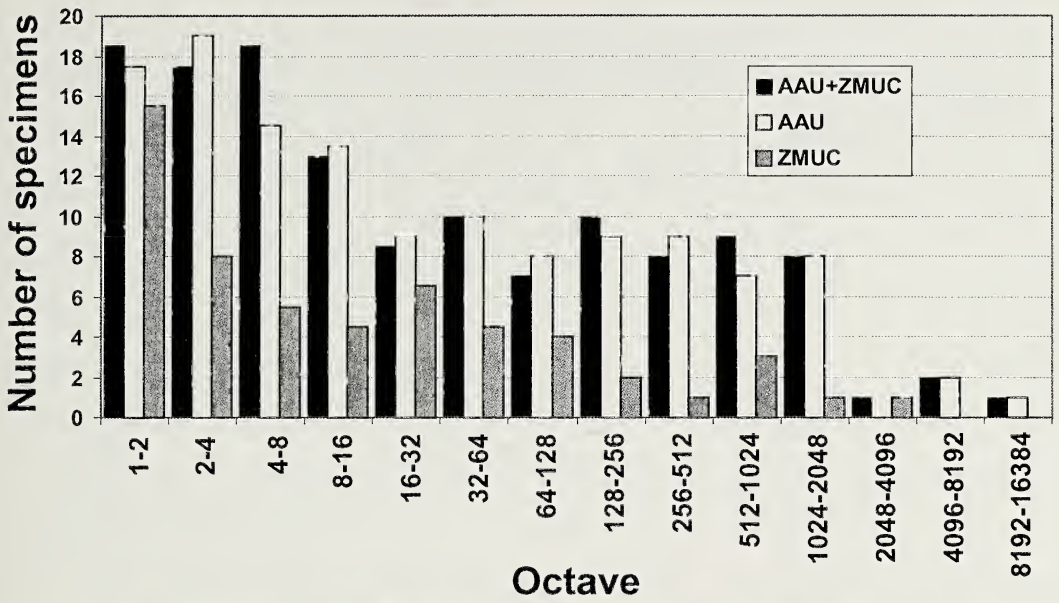


Figure 11.—Lognormal fits for the ZMUC and AAU data alone and combined.

cies and animals were mainly extremely small, unidentifiable juveniles that we excluded from the data. This unparalleled arachnological data set offers a unique opportunity to evaluate critically the more rapid and certainly less thorough ZMUC inventory at the same site. When pooled, the AAU 1969 and 1970 August and September collections total 2,260 adults. August alone comprised 47 species (11 singletons, 7 doubletons) and September 49 species (10 singletons, 12 doubletons); together the list comprised 57 species (16 singletons, 13 doubletons). Considering that for these two months Toft collected only about one fourth

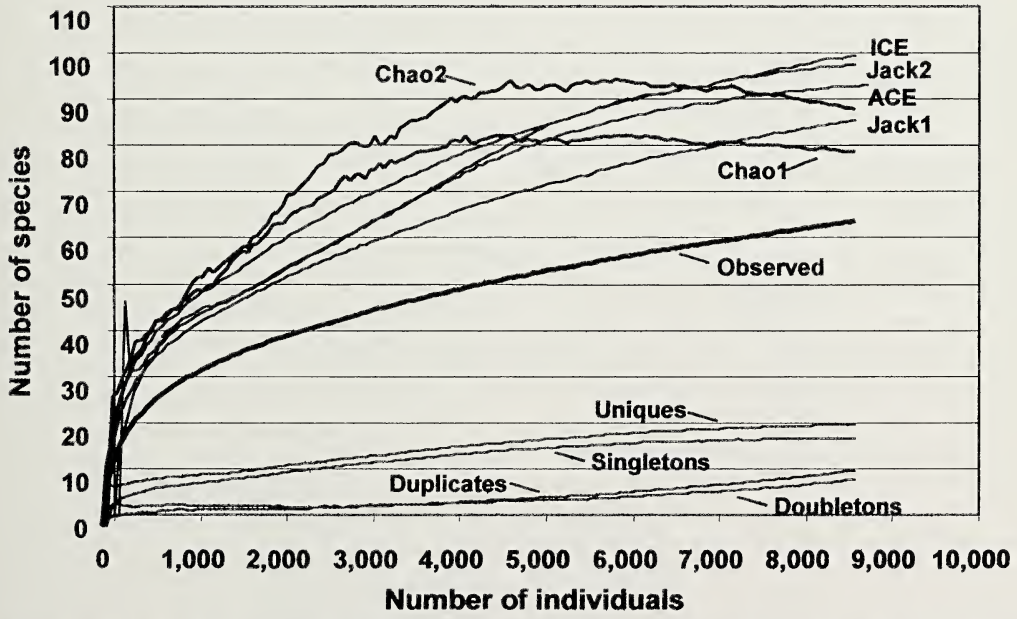


Figure 12.—Curves for observed richness, rare species, and richness estimators for the ZMUC inventory against sampling effort.

Table 2.—Summary values for the AAU inventory at Hestehaven. SD = standard deviation, Spp = species, A = adults, J = juveniles.

	Clubs		Stems		Sweeping		Litter		Pitfalls		Total		Grand
	A	J	A	J	A	J	A	J	A	J	A	J	Total
No. of samples	23		30		21		49		55		178		178
Mean no. of ind./sample	43	91	51	55	122	987	18	25	175	19	87	150	238
SD of ind./sample	36	90	77	57	119	1,134	15	27	201	19	140	492	526
Mean no. of spp./sample	18		10				11		20		17		17
SD spp./sample	7		4.9				3.5		9.7		10		10
Total individuals	988	2,102	1,519	1,644	2,562	20,726	862	1,240	9,602	1,028	15,533	26,740	42,273
Total species	48	39	44	29	60	52	33	37	82	48	130	79	141
Sample intensity	21	54	35	57	43	399	26	34	117	21	119	338	300
Singletons	16	7	14	4	20	6	7	12	20	9	32	11	27
Doubletons	6	2	10	6	9	1	4	0	2	3	12	1	8
% Singletons	33.3	17.9	31.8	13.8	33.3	11.5	21.2	32.4	24.4	18.8	24.6	13.9	19.1
Chao1 estimate	69	51	54	30	82	70	39	—	182	62	173	140	187
% Inventory Completion	69	76	82	96	73	74	84	—	45	78	75	57	76
% Method Bias	−7	0	6	20	−3	−2	8	—	−31	2	−1	−19	0
% Effort Investment	14		5		15		32		34		100		

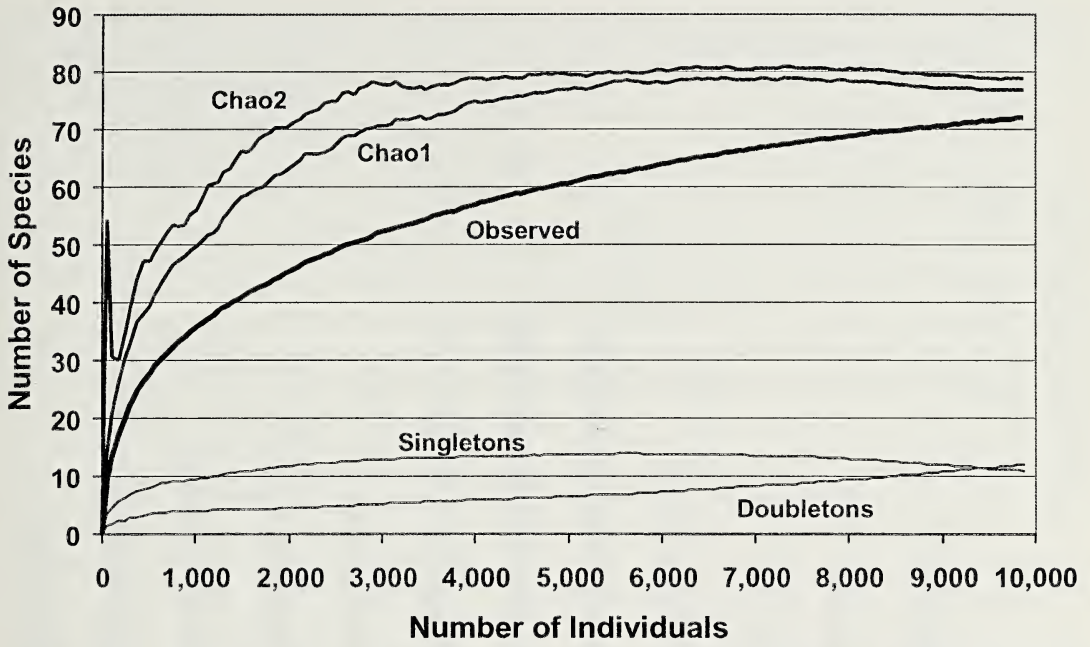


Figure 13.—Curves for observed richness, rare species, and richness estimators for the ZMUC and AAU data for the four week period centered on the ZMUC inventory.

as many adults as the ZMUC total of 8,710, his results are certainly comparable to our 66 species (19 singletons and 12 doubletons). The AAU August and September adult data contained 13 species not found in the ZMUC data, all but two singletons or doubletons, whereas the ZMUC study found 22 species not found by AAU for August–September, all but three singletons or doubletons. If the ZMUC list is compared to the total, annual AAU list, juveniles included, only five ZMUC species are missing from the AAU dataset.

The full two years of AAU data (including juveniles) considered separately and together with the ZMUC data yield a more complete lognormal distribution: the AAU data alone do show a mode one octave to the right of the ZMUC maximum (chi square goodness of fit, $P < 0.975$), and the two datasets combined (chi square goodness of fit, $P < 0.9$) place the mode even further to the right (Fig. 11).

The "best" estimate of the instantaneous richness during the ZMUC inventory is presumably that based on the maximum data available for the seasonal period and the methods used. The ZMUC inventory used neither pitfall traps nor "clubs" but sweeping and litter sifting were common to both studies, and stem traps are quite similar to aerial searching. Excluding the latter methods and taking into consideration annual seasonal variation, we selected all adults collected two weeks before and after the ZMUC sampling dates as the most complete data set for this time period (thus adding 1969–1970 AAU data to the ZMUC study) and calculated richness estimates using this dataset totaling 9,871 adults. Figure 13 shows these curves. The estimates appear substantially better than the ZMUC data alone: the estimator and observed curves are more asymptotic and closer together; the singleton and doubleton curves actually cross. The parametric richness of the adult spider fauna is suggested to be around 80 species.

The observed and Chao1 estimated species richness calculated for each month of the AAU dataset show the summer peak expected in a north temperate fauna (Fig. 14). August–September is substantially past the annual May–June richness peak, judged either by observed or estimated richness. Comparison of estimated to observed richness for the AAU study shows that the level of sampling effort was relatively better early in the year, insufficient to keep up with the May–June peak, recovered somewhat in August–September, and fell off again in October–December.

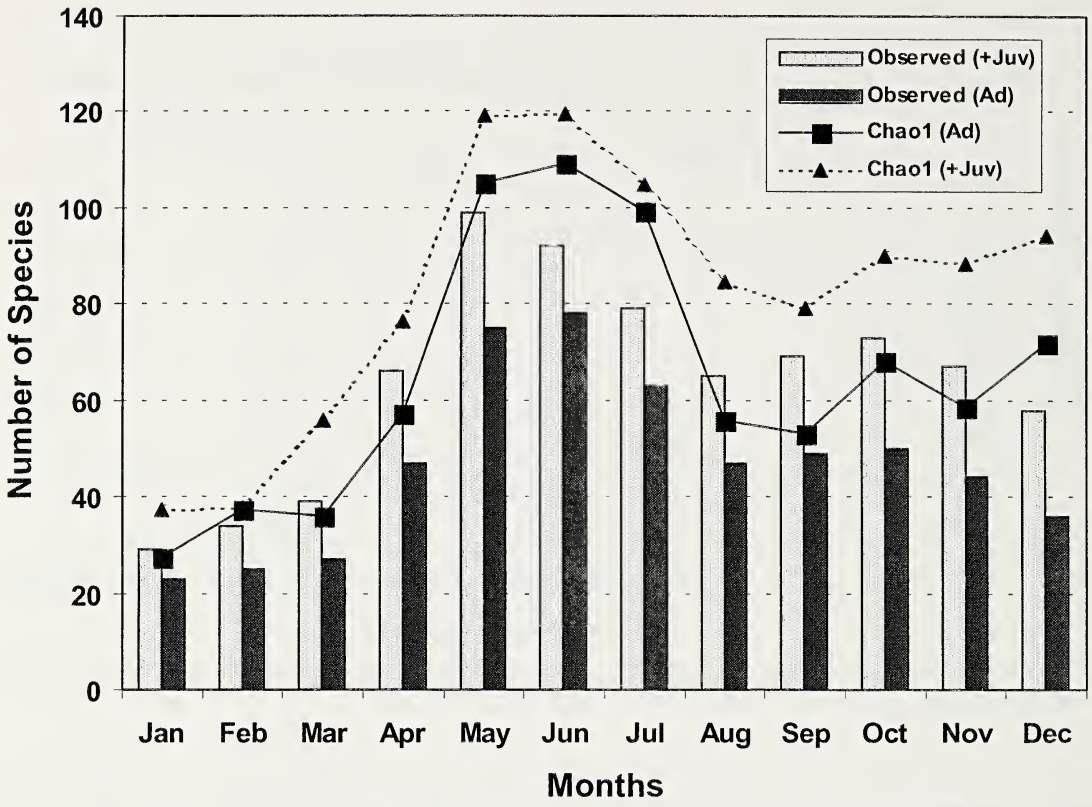


Figure 14.—Total species observed (adults only and including juveniles) for each month of the AAU inventory, with Chao1 estimates based on both partitions.

Monthly-observed adult richness varied from 23 in January to 78 species in June.

Despite the large number of animals collected, the ZMUC inventory still contained 19 singletons and 12 doubletons. The null hypothesis of richness estimation is that rare species indicate undersampling. However, there are at least three alternative explanations for "rare" species besides undersampling bias. Conceptually these are all "edge effects" due to time, method, or space (Longino et al. 2002).

Phenological edge effects.—A phenological edge effect is an individual that is mature outside the normal breeding season of its species. The AAU study aimed principally to reconstruct the life history and phenologies of the spider community at this site. These data (Fig. 15) can be used to "diagnose" which of the rare ZMUC species are "phenological edge effects." For example, 48 of the ZMUC species are normally adult at the time of the inventory, but 13 are typically adult at other times: 12 earlier and one later. We counted a species as a phenological edge effect (as opposed to just being rare) if its total abundance in the AAU study was more than 10, and the time span of adults did not include August or September. Of the 19 singleton and 12 doubleton species in the ZMUC inventory, eight singletons (*Anyphaena accentuata* (Walckenaer 1802), *Araniella curcubitina* (Clerck 1757), *Hypomma cornutum* (Blackwall 1833), *Linyphia hortensis* Sundevall 1830, *Micrargus herbigradus* (Blackwall 1864), *Neriene peltata* (Wider 1834), *Walckenaeria obtusa* (Blackwall 1836), *Pachygnatha listeri* Sundevall 1830) and two doubletons (*Diplocephalus latifrons* (O. P.-Cambridge 1863), *Saaristoa abnormis* (Blackwall 1841)) were out of season and arguably are not evidence of undersampling bias.

Methodological edge effects.—A method edge effect is an individual of a species that typically inhabits a microhabitat not accessed by any of the methods used, or, at least, not efficiently accessed. If a singleton or doubleton ZMUC species was commonly collected

in the AAU study by a method not used in the ZMUC study (i.e. pitfalls or clubs), it is arguably a methodological edge effect and not evidence of undersampling. As above, if the total AAU abundance was more than ten and mainly caught via pitfalls or clubbing, we count it as a methodological edge effect. *Neriene peltata*, *Achaearanea lunata*, and especially *A. accentuata* were all substantially more common in the canopy than in subcanopy strata. Some also showed minor peaks in abundance in sweep samples, suggesting that rarely animals may fall or jump from the canopy and so appear in the herb layer. *Walckenaeria obtusa*, *M. herbigradus*, *P. listeri*, *D. tibiale*, *Lepthyphantes cristatus*, *L. pallidus*, *S. abnormis*, and *D. latifrons* were taken almost exclusively by pitfall traps, although the latter also appeared in litter samples. These 11 species are probably rare in the ZMUC study because they are accessible mainly via methods we omitted, although five were also out of season.

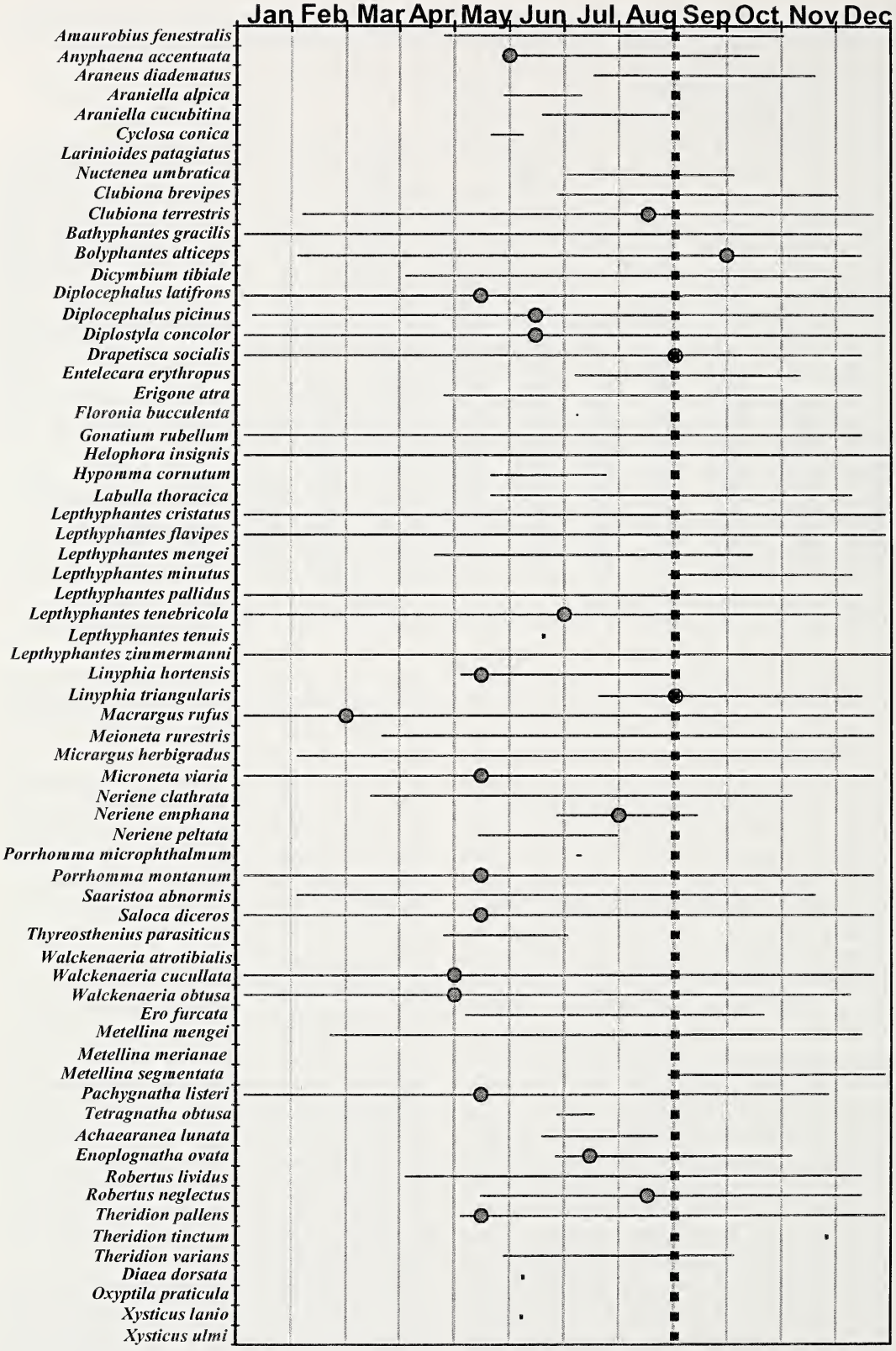
Spatial (habitat) edge effects.—A spatial edge effect is an individual of a species that prefers a habitat not present in the study area. The hectare was fairly uniform, but it had a wet depression at its lower end. *Tetragnatha obtusa* C.L. Koch 1837 may have been rare in both studies because it prefers wetter situations and thus barely enters the plot. Arguably it is not evidence of undersampling. Although not present in the ZMUC study, *Hyptiotes paradoxus* (C.L. Koch 1834) was rare in the AAU study; it prefers the coniferous plantations adjacent to the study hectare and may have been sporadically and unreliably present within study margins. *Metellina merianae* (Scopoli 1763), *Erigone atra* Blackwall 1833 and *Nuctenea umbratica* (Clerck 1757) were rare in both studies, suggesting they may be typical of habitats other than mature beech forest. No Hestehaven "rare" species are truly rare in Denmark.

In sum, of the 19 singleton and 12 doubleton ZMUC species, nine singletons and three doubletons are rare due to edge effects and should not be considered as evidence of undersampling. If these species are excluded from the inventory, and richness estimates recalculated (Fig. 16), the quality of the inventory improves substantially. The estimator curves are definitely asymptotic (at about 4,000 sample size), the observed curve still trails the estimator curve, and the uniques curve is almost flat, and the duplicates curve, unusually, goes to zero.

DISCUSSION

How many species of spiders typically inhabit one hectare of northern European climax beech forest? How much effort is required to answer the question or estimate that number, or how would one know when an observation or estimate was accurate? These questions make sense only if assumptions about temporal and spatial scales are made explicit. The minimum realistic spatial scale that is biologically real is one large enough to include demes of all resident species, species-area effects aside. Biparental organisms, in other words, should be present at least in abundances of two, and for all practical purposes many more. The latter reasoning provides a strong common sense justification for the Chao estimators of species richness, as they trade on the ratio of singletons (biological non-sequiturs) to doubles to correct for undersampling bias. Species literally present in a hectare as singletons don't make biological sense because they can't reproduce and must represent long-distance dispersal; doubletons, for all practical purposes, are the same. Of course, many animals live at spatial scales larger than a hectare, but for spiders, one hectare (100 × 100 m) seems like a reasonable minimum spatial scale because it is unlikely that the breeding population structure of spiders, i.e. the "nearest-neighbor distance," is so dispersed that single hectares are likely to contain one or fewer individuals. A spatial scale of one meter might be appropriate for litter fauna but inappropriate for large cursorial hunters or web weavers. For the latter, as a guess, even 10 m seems excessive. At larger spatial scales the species-area effect will be increasingly important. The Danish national checklist currently stands at 500 species (Scharff 1984). Checklists overestimate current standing diversity because they are cumulative, and not corrected for faunal turnover. Thus, the "instantaneous," ecologically meaningful, richness of spider species in Denmark is probably less.

The "checklist" of Hestehaven listed by Toft (1976) includes 147 identified species. Twenty-three years later the ZMUC study added only five more (*M. merianae* (Scopoli


Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Amaurobius fenestralis
Anyphaena accentuata
Araneus diadematus
Araniella alpica
Araniella cucubitina
Cyclosa conica
Larinioides patagiatus
Nuctenea umbratica
Clubiona brevipes
Clubiona terrestris
Bathyphantes gracilis
Bolyphantes alticeps
Dicymbium tibiale
Diplocephalus latifrons
Diplocephalus picinus
Diplostyla concolor
Drapetisca socialis
Entelecara erythropus
Erigone atra
Floronia bucculenta
Gonatium rubellum
Helophora insignis
Hypomma cornutum
Labulla thoracica
Lepthyphantes cristatus
Lepthyphantes flavipes
Lepthyphantes mengei
Lepthyphantes minutus
Lepthyphantes pallidus
Lepthyphantes tenebricola
Lepthyphantes tenuis
Lepthyphantes zimmermanni
Linyphia hortensis
Linyphia triangularis
Macrargus rufus
Meioneta rurestris
Micrargus herbigradus
Microneta viaria
Neriene clathrata
Neriene emphana
Neriene peltata
Porrhomma microphthalmum
Porrhomma montanum
Saaristoa abnormis
Saloca diceros
Thyreosthenius parasiticus
Walckenaeria atrotibialis
Walckenaeria cucullata
Walckenaeria obtusa
Ero furcata
Metellina mengei
Metellina merianae
Metellina segmentata
Pachygnatha listeri
Tetragnatha obtusa
Achaearanea lunata
Enoplognatha ovata
Robertus lividus
Robertus neglectus
Theridion pallens
Theridion tinctum
Theridion varians
Diaea dorsata
Oxyptila praticula
Xysticus lanio
Xysticus ulmi

1763) , *Larinioides patagiatus* (Clerck 1757), *Ozyptila praticola* (C.L.Koch 1837), *Walckenaeria atrotibialis* (O. P.-Cambridge 1878), *Xysticus ulmi* (Hahn 1831)), all singletons or doubletons except *L. patagiatus* (7 individuals). The absence of faunal additions in 23 years is impressive (we cannot comment on losses): 92% of the ZMUC species were shared with the AAU study. None of the species added by the ZMUC study were present at a relative abundance of more than 0.0008, which also suggests that the fauna is stable over time.

"Instantaneous" Hestehaven richness is much less than 147 species, at least during August–September. The monthly adult richness observed by Toft (1976) ranged from a January low of 23 to a June high of 78 (Fig. 14) and averages 47 ± 18 (sd); the August–September values were 47 and 49. These figures do not include species present as juveniles, which comprised 63% of the spider community in Toft's study. If juveniles are included, monthly richness varies from a January low of 29 to a May high of 99, and averages 64 ± 22 (sd); the August–September values were 65 and 69. Although the average AAU monthly sampling intensity for adults was only 24, the average monthly percent singletons was 27%, essentially the same as in the much more intense 2.5 day ZMUC effort (29%). Although this small sampling effort seems to provide the same percent singletons as the much more intense ZMUC study, our experience is that even small decreases in percent singletons demand logarithmic increases in effort. All the AAU figures still suffer from undersampling bias. The best bias-corrected figures we have are the adult-only estimates for August–September provided by the combined AAU-ZMUC data, which is about 75–80 species (Fig. 13). This figure, then, is predicted to be the ballpark adult spider richness a complete survey would find for this season in this forest using the methods of the ZMUC inventory.

Chao1 estimates of monthly richness from the AAU study, including juveniles, range from a January low of 37 to a June high of 120; August and September values are 85 and 79, respectively (Fig. 14). Because these figures include juveniles, phenological edge effects are minimized, in which case remaining possible biases are method and spatial edge effects. *Hyptiotes paradoxus* is perhaps the only undeniable example of the latter, a species which "should not have been" in the Hestehaven beech wood. The spectrum of methods used by Toft accessed all substrates used by spiders except the high canopy. Both the intense sampling of the ZMUC survey and the effort to identify juveniles by the AAU survey yield essentially the same estimates: the per-hectare August–September standing spider species richness at Hestehaven is probably about 80 species.

If the above is true, the Hestehaven checklist richness of 150 species at first seems paradoxical. If the greatest monthly observed richness is only about 120 species, juveniles included (Fig. 14), where are the remaining 30 species? The most obvious explanation is, again, undersampling bias in the AAU study. Even though Toft identified every animal collected to species, the substantial fraction of singletons in all AAU partitions argues that he missed quite a few species. However, two other explanations should be considered. First, the missing species may not be permanent year-round residents in the sampled hectare. This implies considerable flux of species such that the standing richness indeed fluctuates between about 40 and 120 species, which in turn poses the question of where these species go. As the many hectares of forest adjacent to the study area were essentially identical, mass migration seems unlikely. Second, if the 30 species do remain in the hectare, why is the observed richness not more consistent from month to month? Only two possible explanations seem likely. First, they may vertically migrate into canopy strata that neither inventory accessed. Nielsen (1974c, 1987) found that portions of the arthropod fauna do migrate up and down at this site several times a year. Second, for some portion of the year

←

Figure 15.—Phenology for the 66 species observed in the ZMUC inventory, based on AAU data. Thin horizontal lines give the range during which adults were found (gaps not indicated). Grey indicate peak adult abundances, if present. Squares mark the ZMUC inventory.

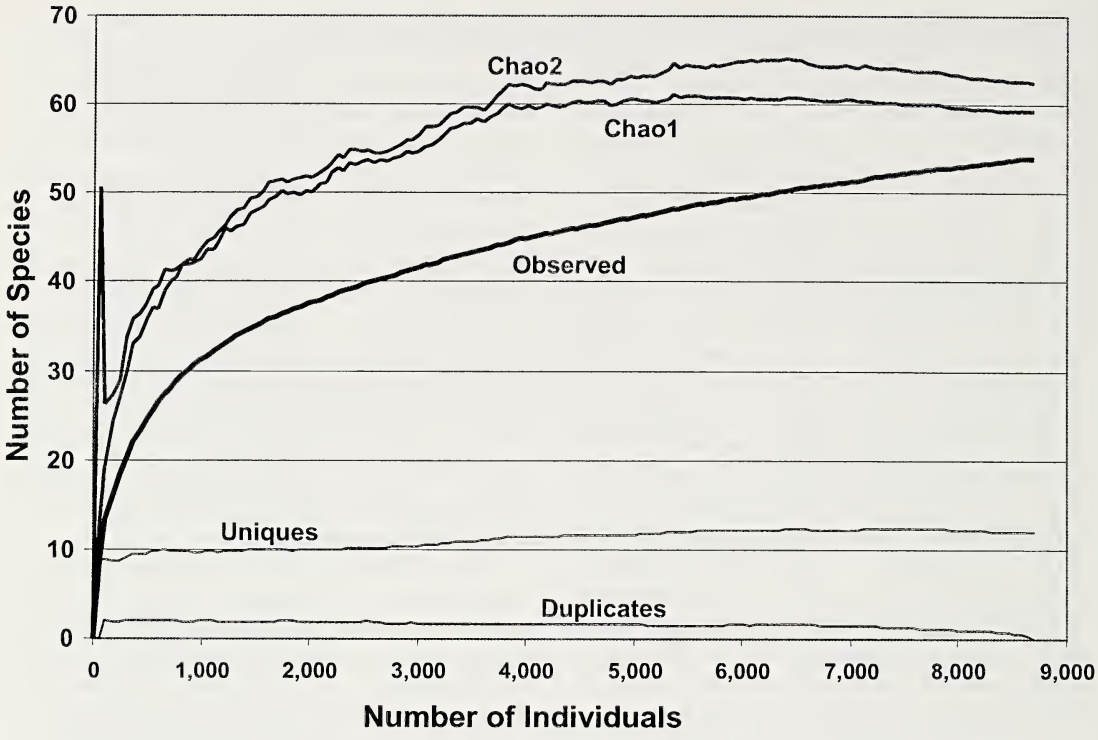


Figure 16.—Curves for observed richness, rare species, and richness estimators for the ZMUC data pruned of artifactually rare species (see text).

these species certainly exist only as eggs or may hide in retreats not accessible to the collecting methods. Thus, the ecologically meaningful late summer spider fauna is probably close to the Chao estimates in Fig. 13—about 80 species.

The AAU and ZMUC studies are best compared on the basis of adults only. For the same time period the AAU sampling intensity was much lower than the ZMUC study (27 vs. 132), but percent singletons was roughly comparable (22 vs. 29%). In terms of specimens collected, the ZMUC study was five times more intense than the AAU effort. The extra ZMUC effort netted about 20 more species, of which 18 were singletons or doubletons—exactly the sort of species the less intense AAU sampling effort would be expected to miss.

Both Figs. 13 & 14 suggest that the ZMUC inventory sampled more spiders than necessary to estimate richness. Perhaps 3–4,000 adults sampled would have been sufficient to estimate species richness, given that the rank-abundance distribution was heavily skewed towards a few extremely abundant species. This depends on collectors being able to recognize accurately the very abundant species in the field.

The heavy reliance on hand-searching during the ZMUC study did not yield significant numbers of species that were missed by the AAU study's reliance on methods less dependent on collector experience. Collector experience does significantly improve the number of species taken per sample, and, usually, experienced collectors do not differ among themselves (see also Sørensen et al. 2002). The collector in Fig. 4 that was classified a priori as experienced did not actually have any experience with this sort of sampling, although he had reportedly collected spiders for many years. How much time a naïve collector requires to become "experienced" is still an open question. Collector experience has only a minor and insignificant effect on numbers of animals. In particular, the maximum number of animals caught per hour (273) greatly exceeds the average (58), which means that observed sample abundances are not limited simply by how fast collectors can collect. Granted that that human collectors as a sampling method will have its own intrinsic bias

(as do all sampling methods), variation in observed abundances probably does reflect gross differences in true relative abundance in the field. Experienced collectors, at any rate, do not catch more species because they catch more animals; the reason is probably that they know more places to look in order to find spiders.

The extreme ecological dominance of *L. triangularis* and *D. socialis* made this inventory less complete than it otherwise would have been. Nearly 50% of the animals collected—quite a practical measure of sampling (and sorting) effort—disappeared into the arguably useless exercise of collecting superfluous specimens. In fact these two species illustrate the extremes of the effects that extreme ecological dominance can have. After one night we truncated collection of *D. socialis* because it was very abundant and easily recognizable. Human collectors can do this. If we had used automated ecological traps, a very great many more *D. socialis* would have died. At the other extreme, two rare species look enough like *L. triangularis* in the field that one cannot reliably distinguish them. Therefore we continued to collect "*L. triangularis*," and eventually collected one *L. hortensis* late in the survey. We sacrificed accuracy of the relative abundance of common species to focus on rare species and to moderate our effect on the fauna. Still, the superabundance of a few species may make it hard for collectors to collect the remainder in an unbiased way. The most abundant spider species in tropical ecosystems rarely exceed 15% of the total (Coddington et al. 1991, 1996; Silva & Coddington 1996; Silva 1996), and that seems mainly to occur at high elevations (Sørensen et al. 2002). Very common species actually may make temperate ecosystems more difficult to survey in some ways than tropical systems.

As expected, collection method and time of day also influence results (Figs. 5–6). Not only are some methods more productive, all methods seem to access different sampling universes (Table 1), which justifies the broadest possible spectrum of collecting methods in faunal inventories that aim to be complete.

Sampling methods access different components of the fauna. Equal effort among methods implicitly assumes that all methods are equally efficient, and that the sampling universes particular to each method are roughly the same size. These assumptions are clearly unrealistic, and thus to minimize sampling bias, inventories should differentially allocate effort among methods, if a goal of the inventory is to sample the community with as little bias as possible. We suggest that inventory completion is a reasonable, albeit imperfect, statistic to measure this bias. It implies that the optimal allocation strategy would yield similar inventory completion measures for all inventory partitions, whether by method, time of day, or other partitions. Thus, all partitions might be undersampled, but they would be, in some sense, "equally" under-sampled. The ZMUC study emphasized cryptic and ground searching in anticipation of large numbers of ground-dwelling linyphiid species. The results suggest that the cryptic fauna was relatively over-sampled, and the ground fauna relatively undersampled, which in turn suggests that the sample of the overall spider community we obtained is biased in particular ways, although not as much as it would have been had the sampling allocation been more nearly uniform. One could, for example, calculate richness for various taxa and assess how well the methods sampled those taxa. If the sampling regime had lasted more days, litter and pitfall samples could have been added without diminishing the amount of time for collector-based sampling. We certainly support using as many techniques as resources permit. Allocation of sampling effort across methods is a serious problem. Although ideally the sample should reflect the parametric community, and in theory richness estimators should identify departures from that ideal, we do not know if the inventory completion statistics are robust from one study or region to another. If a given investment in, say, sweeping, produces wildly different and unpredictable results from place to place, year-to-year in the same place, or study-to-study, it will not be a useful analytical technique.

Grossly different numbers of samples between methods or times of day inevitably produce highly unbalanced statistical designs for analysis of variance. However, the natural history logic of investing more in productive as opposed to less productive methods in our view outweighs the analytical convenience of a completely balanced design. First, the statistical differences we detected in this study are large ($P < 0.00$) and are unlikely to dis-

appear in a balanced design. Second, modern statistical packages can correct much better for unbalanced designs than formerly. Third, if necessary one can include only the first N samples in each analysis of variance cell, where N is the global minimum cell size. This provides an unambiguous way to test sampling effects while still freeing the investigator to allocate sampling effort in the way best calculated to access efficiently and accurately the total fauna.

This study demonstrates design and analytical methods by which undersampling bias in terrestrial arthropod surveys can be detected and measured. The evidence for severe undersampling bias in arthropod surveys is pervasive if measured by percent singletons. Large samples do not indicate a thorough inventory if the inventory scope was broad. In spiders, for example, the fogging of the canopy of a single tree from Manu National Park, Perú by T. L. Erwin yielded 222 adult spiders of 124 species, 63% of which were singletons, and multiple tree canopies from Tambopata, Peru, yielded 1,821 adult spiders of 645 species, 55% of which were singletons (Coddington, unpublished data). Silva (1996) reported 43% singletons in a collection of 5,895 adults of 1,140 species from Samiria, Peru, collected mostly by fogging. A recent spider canopy study from Tanzania had 23% singletons (Sørenson 2003). Other authors often report diversity statistics for fogging samples rather than raw numbers, but because Fisher's alpha approximates the number of singletons, Russell-Smith and Stork (1994) must have found an average of about 45% singleton spider species in fogging samples at four stations along an elevational transect in Sulawesi. Subcanopy manual collecting in Manu yielded 2,616 adults of 498 species with 42% singletons (Silva and Coddington 1996). Three points along an elevational transect in Bolivia averaged 44% singletons in subcanopy faunas (Coddington et al. 1991, 1996). Kuntner and Baxter (1997) found 54% singletons in subcanopy collections in Slovenia. Singleton percentages for spider inventories are not out of line with terrestrial arthropods generally. Novotny and Basset (2000) collected over 80,000 homopterans, but these comprised over 1,000 species, of which 27% were singletons. Toft (1976) and this study together collected 50,983 spiders of 146 species, but again 27% were singletons. Basset et al. (1996) collected 4,696 individuals of 391 species of beetles, and percent singletons was 39% (Basset 1997). Basset and Kitching (1991) collected 20,500 individuals of 759 subcanopy and canopy species but 36% were singletons. The canopy fraction was higher at 45%; among spiders it was 42%. Allison et al. (1997) sampled 3,977 individuals of 481 species of beetles, but 46% were singletons. Erwin (1997) reports collecting 15,869 Peruvian beetles of 3,429 species of which 50% were singletons. Janzen and Schoener (1968) reported 65% singletons in their arthropod collections from all of Costa Rica, and Noyes (1989) reported 60% in Chalcidoidea from Sulawesi. Monteith and Davies (1984) likewise found 40% singletons during a month-long survey of Queensland rainforest. In relative abundance distributions such as these doubletons are very probably about half the singletons, so something like 50–70% of the species found in many "state of the art" arthropod surveys are known from two or fewer individuals.

This study was able to explain only about a third of the rare species as artifacts of one sort or another. The remainders imply that even after intense sampling, observed richness understated true richness by at least 20%. The relative abundances of the species found by ZMUC and missed by AAU for August–September is consistent with the hypothesis that most "rare" species (singletons) in terrestrial arthropod surveys are legitimate members of the community. The tendency to ignore rare species as "tourists" should be viewed with skepticism (Stork & Samways 1995). These estimates formally are all lower bounds (Bunge & Fitzpatrick 1993; Colwell & Coddington 1994), so the actual situation is probably worse. Figures 12, 13 and 16 show that in practice estimators' asymptote only when about two-thirds or more of the species are already observed. In sum, both statistical species richness estimators and the observed richness are negatively biased with respect to parametric community richness for most of the time course of an inventory. Richness estimates statistically corrected for undersampling bias are nevertheless more accurate than the raw, observed richness, and, depending on the degree of accuracy required, probably almost never show significant positive bias in practice.

Because return-on-effort in inventories is inevitably curvilinear, direct comparisons of richness values between sites are likely to be fraught with bias and error (Gotelli & Colwell 2001). This study also shows that for the first 2,000 or so specimens as a measure of effort, even the most aggressive richness estimators are still strongly and negatively biased. Considering that a sample of 2,000 animals from a parametric community richness of about 80 species still represents a sampling intensity of 25, and that sampling intensities of less than 10 are probably typical of most work, one must question the prevailing paradigm of spreading arthropod inventory resources as thinly as possible in pursuit of broad goals and diverse taxa. It is the rare terrestrial arthropod inventory taxon that does not have twice, or even 10 times the anticipated diversity as any sympatric vertebrate group, and arthropod surveys generally make do with less resource than vertebrate surveys. Masters theses that envisage a single student sampling a diverse taxon once or twice a month over an annual cycle in a seasonal environment is almost certain to result in data so sparse that absence due to undersampling bias will be indistinguishable from that due to biologically interesting variation (McArdle & Gaston 1993). Of course, not all surveys aim to measure or estimate richness, but comparative species richness is increasingly the most important datum, at least initially, in biodiversity conservation (Mittermeier et al. 1998). Nevertheless, until very recently, manuals and treatments of inventory methods rarely mention undersampling bias (Hayek & Buzas 1997; Stork & Samways 1995), but see (Leitner & Turner 2001). Compared to the initial costs of mounting the survey to begin with, designing and funding it well enough to secure verifiably reliable data seems at most a marginal cost increase. If the conservation of biodiversity depends on reliable data, both funding agencies and the designers of inventory protocols should reconsider prevailing practices.

ACKNOWLEDGMENTS

We would particularly and especially like to thank Søren Toft for providing access to his original data from Hestehaven and for practical help in connection with the inventory. We thank Karsten Laursen and Michael Stoltze from the National Environmental Research Institute, Rønde, for permission to work in the Hestehaven forest and for logistic help while in the field. The Natural History Museum in Århus kindly provided free lodging at the field station "Molslaboratoriet", Femmøller, Ebeltoft.

We would like to thank the other members of our field team in Hestehaven, Per Christiansen, Jonas Krat, Søren Langemark and Line L. Sørensen, for collecting assistance. Specimens were sorted and identified by Per de Place Bjørn, Sidsel Larsen, Søren Langemark, Søren Jensen, Nikolaj Scharff, and Ole Gudik-Sørensen. We are indebted to Line L. Sørensen, Maggie Hodge, and two anonymous reviewers for comments on an earlier draft of this papers.

This study was supported in part by grants from the Zoological Museum, University of Copenhagen, the Danish Natural Science Research Council (N.Scharff: grant nos. 11-7440, 11-8038, 11-9877, 9300106 and 9502155) and grants from the Smithsonian Institution (Neotropical Lowlands Program and Biological Diversity of Latin America to Coddington) and the National Science Foundation (DEB-9707744 to Coddington and DEB-9712353 to Hormiga and Coddington).

LITERATURE CITED

Allison, A., G.A. Samuelson & S.E. Miller. 1997. Patterns of beetle species diversity in Castanopsis acuminatissima (Fagaceae) trees studied with canopy fogging in mid-montane New Guinea rainforest. Pp. 224–236. *In* Canopy Arthropods (N.E. Stork, J. Adis & R.K. Didham, ed.). Chapman & Hall, London.

Basset, Y. 1997. Species abundance and body size relationships in insect herbivores associated with New Guinea forest trees, with particular reference to host specificity. Pp. 237—264. *In* Canopy Arthropods (N.E. Stork, J. Adis & R.K. Didham, ed.). Chapman & Hall, London.

Basset, Y., & R.L. Kitching. 1991. Species number, species abundance and body length of arboreal arthropods associated with a rainforest tree. Ecological Entomology 16:391–402.

Basset, Y., G.A. Samuelson, A. Allison & S.E. Miller. 1996. How many species of host-specific insects feed on a species of tropical tree. Biological Journal of the Linnean Society 59:201–216.

Bliss, C.I. 1966. An analysis of some insect trap records. Pp. 385–397. *In* Classical and Contagious Discrete Distributions (G.P. Patil., ed.). Statistical Publishing Society, Calcutta.

Bunge, J. & M. Fitzpatrick. 1993. Estimating the

number of species: a review. Journal of the American Statistical Association 88(421):364–373.

Coddington, J.A., C.E. Griswold, D. Silva, D. Peñaranda & S. Larcher. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pp. 44–60. *In* The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology. (E.C. Dudley, ed.). Dioscorides Press, Portland, Oregon.

Coddington, J.A., L.H. Young & F.A. Coyle. 1996. Estimating spider species richness in a southern Appalachian cove hardwood forest. The Journal of Arachnology 24:111–124.

Colwell, R.K. 2000. EstimateS: Statistical estimation of species richness and shared species from samples. Version 6.01. User's Guide and application available from http://viceroy.eeb.uconn.edu/estimates.

Colwell, R.K. & J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transaction of the Royal Society London, series B. 345:101–118.

Dobyns, J.R. 1997. Effects of sampling intensity on the collection of spider (Araneae) species and the estimation of species richness. Environmental Entomology 26(2):150–162.

Erwin, T. L. 1983. Tropical forest canopies: the last biotic frontier. Bulletin of the Entomological Society of America 30:14–19.

Erwin, T.L. 1997. Biodiversity at its utmost: tropical forest beetles. Pp. 27–40. *In* Biodiversity II (M.L. Reaka-Kudla, D.E. Wilson & E.O. Wilson, ed.). Joseph Henry Press, Washington, D.C.

Gotelli, N.J. & R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Groombridge, B. 1992. Global Biodiversity: Status of the Earth's Living Resources. Chapman & Hall, London.

Hayek, L.-A.C. & M.A. Buzas. 1997. Surveying Natural Populations. Columbia Univ. Press, New York.

Heyer, W.R., J. A. Coddington, W.J. Kress, P. Acevedo, D. Cole, T.L. Erwin, B.J. Meggers, M.G. Pogue, R.W. Thorington, R.P. Vari, M.J. Weitzman & S.H. Weitzman. 1999. Amazonian biotic data and conservation decisions. Ciência e Cultura 51(5–6):372–385.

Janzen, D.H. & T.W. Schoener. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49:96–110.

Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F Noss, & M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7:796–808.

Kuntner, M. & I.H. Baxter. 1997. A preliminary investigation of spider species richness in an eastern Slovenian broadleaf forest. Pp. 173–182. *In.* Proceedings of the 16th European Colloquium of Arachnology, Siedlce, Poland.

Larsen, S. & T.D. Rasmussen. 1999. Rapid assesement of spider species richness in the Arctic (Disko, West Greenland). Berichte zur Polarforschung 330:76–77.

Leitner, W. & W.R. Turner. 2001. Measurement and Analysis of Biodiversity. Pp. 123–144. *In* Encyclopedia of Biodiversity (S.A. Levin, ed.). Academic Press, New York.

Lobo, J.M. & M.E. Favila. 1999. Different ways of constructing octaves and their consequences on the prevalence of the bimodal species abundance distribution. Oikos 87:321–326.

Longino, J.T. 1994. How to measure arthropod diversity in a tropical rainforest. Biology International 28:3–13.

Longino, J.T., J. A. Coddington, & R.K. Colwell. 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. Ecology 83:689–702.

Ludwig, J.A. & J.F. Reynolds. 1988. Statistical Ecology: a primer on methods and computing. John Wiley and Sons, New York.

May, R.M. 1975. Patterns of species abundance and diversity. Pp. 81–120. *In* Cody, M.L. & Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Bellknap Press of Harvard University, Cambridge, USA.

May, R.M. 1978. The dynamics and diversity of insect faunas. In: Mound, L.A. & Waloff, N. (Eds.), Diversity of insect Faunas: 9th Symposium of the Royal Entomological Society. Pp. 188–204., Blackwll, Oxford. 1993

McArdle, B.H. & K.J. Gaston. 1993. The temporal variability of populations. Oikos 67:187–191.

McKamey, S.H. 1999. Biodiversity of tropical Homoptera, with the first data from Africa. American Entomologist 45:213–222.

Mittermeier, R., P. Gil & C. Goettsch-Mittermeier. 1998. Megadiversity: Earth's Biologically Wealthiest Nations. Cemex, S.A., Prado Norte.

Monteith, G.B. & V.T. Davies. 1984. Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. Pp. 402–414. *In* Australian National Rainforest Study Report, Vol. 1. Proceedings of a workshop on the past present and future of Australian rainforests (G.L. Werren & A.P. Kershaw, eds.). Geography Dept. Monash Univ., Melbourne.

Nielsen, B.O. 1974a. The phenology of beech canopy insects in Denmark. Videnskabelige Med-

delelser fra dansk naturhistorisk Forening 137: 95–124.

Nielsen, B.O. 1974b. En undersøgelse over snudebillefaunaen (Curculionidae) i en dansk bøgeskov (Studies on the weevils (Curculionidae) of a Danish beech forest). Entomologiske Meddelelser 42:169–188.

Nielsen, B.O. 1974c. Registrering af insektaktivitet på bøgestammer ved hjælp af fangtragte (A record of insect activity on beech stems (*Fagus silvatica* L.) by means of arboreal photoeclectors). Entomologiske Meddelelser 42:1–18.

Nielsen, B.O. 1975. Nedbankning med køller anvendt som indamlingsmetode på bøg (Sampling of arboreal insects from beech by beating tree stems with clubs). Entomologiske Meddelelser 43:37–61.

Nielsen, B.O. 1977. Seasonal and annual variation in litter fall in a beech stand 1967–1975. Det forstlige Forsøgsvæsen 35(1):17–38.

Nielsen, B.O. 1978a. Above ground food resources and herbivory in a beech forest ecosystem. Oikos 31:273–279.

Nielsen, B.O. 1978b. Food resource partition in the beech leaf-feeding guild. Ecological Entomology 3:193–201.

Nielsen, B.O. 1987. Vertical distribution of insect populations in the free air space of beech woodland. Entomologiske Meddelelser 54:169–178.

Norris, K.C. 1999. Quantifying change through time in spider assemblages: sampling methods, indices and sources of error. Journal of Insect Conservation 3:309–325.

Novotny, V. & Y. Basset. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. Oikos 89:564–572.

Noyes, J.S. 1989. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. Ecological Entomology 14:197–207.

Peterson, A.T. & N.A. Slade. 1998. Extrapolating inventory results into biodiversity estimates and the importance of stopping rules. Diversity and Distribution 4:95–105.

Platnick, N. I. 2002. The world spider catalog, version 2.5. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog81–87/index.html.

Prendergast, J.R., R.M. Quinn, J.H. Lawton, B.C. Eversham & D.W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365:335–337.

Preston, F.W. 1948. The commonness and rarity of species. Ecology 29:254–283.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. Ecology 43:185–215&410–432.

Rasmussen, S., M.K. Nielsen & J.P.N. Hansen. 1982. The climate of a Danish beech wood, Hestehaven, eastern Jutland. Holarctic Ecology 5: 412–419.

Russell-Smith, A. & N. E. Stork. 1994. Abundance and diversity of spiders from the canopy of tropical rainforests with particular reference to Sulawesi, Indonesia. J. Tropical Ecology 10:545–558.

Russell-Smith, A. & N.E. Stork. 1995. Composition of spider communities in the canopies of rainforest trees in Borneo. Journal of Tropical Ecology 11:223–235.

Scharff, N. 1984. Edderkopper (Araneae). Pp. 8–10. *In* Entomologisk Litteratur—En hjælp til studiet af den danske insektfauna (O. Lomholdt, P. Nielsen & K. Schnack, eds.). Entomologiske Meddelelser 51(1–2), Copenhagen.

Silva, D. 1996. Species composition and community structure of Peruvian rainforest spiders: a case study from a seasonally inundated forest along the Samiria River. Revue Suisse de Zoologie vol. hors serie:597–610.

Silva, D. & J.A. Coddington. 1996. Spiders of Pakitza (Madre de Dios, Perú): Species richness and notes on community structure. Pp. 253–311. *In* The Biodiversity of Southeastern Perú. (D.E. Wilson & A. Sandoval, eds.). Smithsonian Institution, Washington D.C.

SPSS Inc. 1999. Systat version 9. SPSS Inc., 233 South Wacker Drive, Chicago, USA (www.systat.com).

Stork, N.E. & M.J. Samways. 1995. Inventorying and Monitoring. Pp. 453–543. *In* Global Biodiversity Assessment (V.H. Heywood, ed.). Cambridge University Press, Cambridge.

Sørensen, L.L., 2003. Stratification of the spider fauna in a Tanzanian forest. Pp 92–101: *In* Arthropods of Tropical Forests: Spatiotemporal Dynamics and Resource Use in the Canopy (Y. Basset, V. Novotny, S.E. Miller & R.L. Kitching eds.) Cambridge University Press.

Sørensen, L.L., J.A. Coddington & N. Scharff. 2002. Inventorying and estimating sub-canopy spider diversity using semi-quantitative sampling methods in an Afromontane forest. Environmental Entomology 31:319–330.

Taylor, L.R. 1978. Bates, Williams, Hutchinson—a varity of diversities. Pp. 1–18. *In* Diversity of Insect Faunas: 9th Symposium of the Royal Entomological Society (L.A. Mound, & N. Waloff, eds.), Blackwell, Oxford, UK.

Thamdrup, H.M., B.O. Nielsen & H. Petersen. 1975. The Hestehave Project. Pp. 24–33. *In* IBP Final Report. Scandinavian Countries Denmark, Finland, Norway, and Sweden. Scandinavian National Committees of the International Biological Programme (IBP), Oslo.

Toft, S. 1976. Life-histories of spiders in a Danish beech wood. Natura Jutlandica 19:5–40.

Toft, S. 1978. Phenology of some Danish Beechwood Spiders. Natura Jutlandica 20:285–304.

Toft, S. 1983. On identifying juvenile spiders: Some general considerations and an example (Genus *Meta*). Verh. naturwiss. Ver. Hamburg (NF) 26: 211–216.

Toti, D.S., F.A. Coyle & J.A. Miller. 2000. A structured inventory of Appalachian grass bald and heath bald spider assemblages and a test of species richness estimator performance. Journal of Arachnology 28:329–345.

Walter B.A. & J-L. Martin. 2001. Species richness estimation of bird communities: how to control for sampling effort. Ibis 143:413–419.

Manuscript received 15 January 2002, revised 31 October 2002.

Appendix 1.—Species and number of adult spiders collected in Hestehaven, Denmark; Collection method and time of day indicated by: D = (Day; N = Night); Nomenclature following Platnick (2002).

Taxon	Collection method										
	Aerial		Beating		Cryptic		Ground		Sweeping		
	D	N	D	N	D	N	D	N	D	N	Total
Anyphaenidae											
Anyphaena accentuata (Walckenaer 1802)				1							1
Amaurobiidae											
Amaurobius fenestralis (Stroem 1768)		5			23	2	5	8		1	44
Araneidae											
Araneus diadematus Clerck 1757	6	35	6			1	3	4	18	12	85
Araniella alpica (L. Koch 1869)									1		1
Araniella cucurbitina (Clerck 1757)		1									1
Cyclosa conica (Pallas 1772)							1		1		2
Larinioides patagiatus (Clerck 1757)		4						1		2	7
Nuctenea umbratica (Clerck 1757)										1	1
Clubionidae											
Clubiona brevipes Blackwall 1841			1	6				3		1	11
Clubiona terrestris Westring 1851		3	7		209	7	148	190	12	92	668
Linyphiidae											
Bathyphantes gracilis (Blackwall 1841)									4		4
Bolyphantes alticeps (Sundevall 1833)					7	2	18	5	4	4	40
Dicymbium tibiale (Blackwall 1836)					2						2
Diplocephalus latifrons (O.P.-Cambridge 1863)					2						2
Diplocephalus picinus (Blackwall 1841)					15	1	3	1		1	21
Diplostyla concolor (Wider 1834)					14			3			17
Drapetisca socialis (Sundevall 1833)	204	1501	25	2	29		95	172	11	7	2046
Entelecara erythropus (Westring 1851)					1						1
Erigone atra Blackwall 1833									2		2
Floronia bucculenta (Clerck 1757)								2			2
Gonatium rubellum (Blackwall 1841)			1		11		6	4	2	1	25
Helophora insignis (Blackwall 1841)	9	21	139	39	80	8	111	60	188	193	848

Appendix 1.—Continued.

Taxon	Collection method										
	Aerial		Beating		Cryptic		Ground		Sweeping		
	D	N	D	N	D	N	D	N	D	N	Total
Hypomma cornutum (Blackwall 1833)										1	1
Labulla thoracica (Wider 1834)	1	40	4		53	9	231	391	2	3	734
Lepthyphantes cristatus (Menge 1866)							1	1			2
Lepthyphantes flavipes (Blackwall 1854)					56	2	82	90	8	9	247
Lepthyphantes mengei Kulczinski 1887								4			4
Lepthyphantes minutus (Blackwall 1833)		3					4	31			38
Lepthyphantes pallidus (O.P.-Cambridge 1871)					2						2
Lepthyphantes tenebricola (Wider 1834)					12		23	74			109
Lepthyphantes tenuis (Blackwall 1852)								1	3	4	8
Lepthyphantes zimmermanni Bertkau 1890		2	2	3	81	9	127	115	8	23	370
Linyphia hortensis Sundevall 1830							1				1
Linyphia triangularis (Clerck 1757)	110	440	91	11	55	2	303	228	536	359	2135
Macrargus rufus (Wider 1834)					13		3	2			18
Meioneta rurestris (C.L. Koch 1836)									7		7
Micrargus herbigradus (Blackwall 1854)					1						1
Microneta viaria (Blackwall 1841)					95	7	8	1			111
Neriene clathrata (Sundevall 1830)					1		1				2
Neriene emphana (Walckenaer 1841)		8	1								9
Neriene peltata (Wider 1834)		1									1
Porrhomma microphthalmum (O.P.-Cambridge 1871)								1			1
Porrhomma montanum Jackson 1913					6						6
Saaristoa abnormis (Blackwall 1841)					2						2
Saloca diceros (O.P.-Cambridge 1871)	4				14						18
Thyreosthenius parasiticus (Westring 1851)					26		1				27
Walckenaeria atrotibialis O.P.-Cambridge 1878							1				1
Walckenaeria cucullata (C.L. Koch 1836)	2				27	1	1	1			32
Walckenaeria obtusa Blackwall 1836					1						1
Mimetidae											
Ero furcata (Villers 1789)					1					1	1

Appendix 1.—Continued.

Taxon	Collection method										
	Aerial		Beating		Cryptic		Ground		Sweeping		
	D	N	D	N	D	N	D	N	D	N	Total
Tetragnathidae											
Metellina mengei (Blackwall 1869)	3	7	5				5	9	45	19	93
Metellina merianae (Scopoli 1763)					1			1			2
Metellina segmentata (Clerck 1757)	19	81	25	12	20	1	39	73	196	156	622
Pachygnatha listeri Sundevall 1830							1				1
Tetragnatha obtusa C.L. Koch 1837										1	1
Theridiidae											
Achaearanea lunata (Clerck 1757)		1						1			2
Enoplognatha ovata (Clerck 1757)		1							1	3	5
Paidiscura pallens (Blackwall 1834)	4	5	10		3				10	5	37
Robertus lividus (Blackwall 1836)	2				9	1					12
Robertus neglectus (O.P.-Cambridge 1871)			12		15		3	9	92	75	206
Theridion tinctum (Walckenaer 1802)		1	1								2
Theridion varians Hahn 1833		2	1								3
Thomisidae											
Diaea dorsata (Fabricius 1777)										1	1
Ozyptila praticula (C.L. Koch 1837)							1				1
Xysticus lanio (C.L. Koch 1835)							1				1
Xysticus ulmi (Hahn 1831)										1	1
Grand Total	364	2162	331	74	887	53	1227	1486	1151	975	8710

2003. The Journal of Arachnology 31:274–277

OBSERVATIONS OF *THEOTIMA MINUTISSIMUS* (ARANEAE, OCHYROCERATIDAE), A PARTHENOGENETIC SPIDER

Robert L. Edwards: Box 505, Woods Hole, Massachusetts 02543, USA.

Eric H. Edwards: 45 Canterbury Lane, East Falmouth, Massachusetts 02536, USA.

Annabel D. Edwards: Massachusetts General Hospital, Department of Anesthesia, Boston, Massachusetts 02114, USA.

ABSTRACT. It has been suggested by several authorities that at least one species of spider of the genus *Theotima*, family Ochyroceratidae, occurring in tropical regions in South Africa, the Caribbean and Asia may be parthenogenetic. *Theotima minutissimus* is particularly abundant in the tropical rainforest leaf litter on El Yunque, Puerto Rico. While many hundreds of specimens have been collected over many years, none has been a male. To examine the possibility that this small species, ± 0.9 mm body length, is parthenogenetic, live specimens were collected and maintained in the laboratory. A second generation spiderling, raised separately, produced viable progeny.

Keywords: Parthenogenesis, spider, tropical rainforest, leaf litter, *Wolbachia*

The six-eyed spider family Ochyroceratidae is found in subtropical and tropical regions around the world and is especially species rich in the Indo-Pacific. There are ten genera found worldwide with four known from the western hemisphere; *Fageicera* and *Speocera* recorded only from Cuba, *Ochyrocera* in the Caribbean region and Brazil, and *Theotima*. *Theotima minutissimus*, originally described as *Oonopinus minutissimus* Petrunkevitch 1929, occurs in the Caribbean region, also in the Indo-Pacific and possibly Africa as well (Platnick 1997). Females of this family typically carry their eggs until they hatch in their chelicerae. Two undescribed sympatric species of *Ochyrocera* occur in forest leaf litter in Puerto Rico. There is little published information available on the life history of any of these spiders.

Theotima minutissimus is abundant in the Caribbean National Forest, El Yunque, Luquillo, Puerto Rico. Its preferred habitat is litter composed of smaller leaves in second growth forests with understory shrubs or in those forests with damper and more easily decayed leaves such as mahogany (*Swietenia macrophylla* King) or bamboo (*Bambusa vulgaris* Schrad.). *T. minutissimus* prefers elevations less than 800 m. From 1992–2001, we collected more than 700 0.25 m^2 litter samples. These samples were taken in all the principal habitats on El Junque. The abundance of *T. minutissimus* in the samples ranged from 5–460 individuals m^{-2}. An earlier study in the Tabonuco forest (*Dacryodes excelsa* Vahl), demonstrated a range of abundance of 43–166 individuals m^{-2}, with a mean annual density of 74 (Pfeiffer 1996). Only in the Tabanuco forest was the abundance of *T. minutissimus* consistently exceeded by another litter spider species, *Modisimus montanus* Petrunkevitch 1929.

The number of penultimate and adult *Theotima minutissimus* specimens examined to date exceeds 1,000. No male has ever been found. The male palpi of other members of the family Ochyroceratidae are distinctively different from those of the female (see for example fig. 1, p. 83 in Emerit & Lopez 1985) and are readily distinguishable even in the penultimate instar. The absence of any *T. minutissimus* showing such palpi leads to the supposition that this spider could be parthenogenetic. Machado (1964) became convinced that a species of the genus *Theotima* of the feminina group in Africa in the Congo and Angola was parthenogenetic. Deeleman-Reinhold (1995) subsequently reported what appears to be the same species of *T. minutissimus* from Panama, the Philippines, Borneo, Indonesia,

Sumatra, Thailand and Guam. She noted, in addition to not finding males, that "The most salient feature is the paired lightly sclerotized arch on the lateral margin of the epigastric opening: the "spermathecae" are very thin walled and easily shift position." This report implies a potentially faulty genital apparatus. Deeleman-Reinhold also suggested that this spider may be parthenogenetic.

To determine whether or not *Theotima minutissimus* was in fact parthenogenetic, on 8 February 2001, 22 females judged to be either mature or penultimate were collected and placed separately in small petri dishes (Fisher No. 09-75-53C, 50 mm diameter Petri Dish with absorbent pad). Each pad was moistened with two drops of water, and 10 or more entomobryid springtails (*Sinella curviseta* Brook) were added as food. The dishes were then placed in a larger plastic container containing a moistened sponge to help maintain humidity. The temperature was maintained between 19–22 °C.

Unless the spider positioned itself on the top of the petri dish, venter side up, it was not possible to determine whether or not it was an adult. There appear to be at least 5 instars that gradually increase in pigmentation from the third instar on, but with no obvious changes in pigmentation, body structure or the appearance of the epigynum between the penultimate and adult stage. Twenty adults averaged slightly less than 1 mm (0.79–0.98) and 20 penultimate 0.76 mm (0.69–0.83) in body length. In the petri dish any exuviae or remains of deceased spiders were quickly scavenged by the springtails and seldom seen.

Female *Theotima minutissimus* carry their eggs in a bundle in their chelicerae until the spiderlings are fully developed and capable of moving about on their own. The number of eggs varies from 1–9; 4–6 eggs per clutch were most common. Eggs were produced by 17 of the 22 captive females with egg numbers varying from 1–9. In three cases eggs were abandoned before they developed. In three other cases females produced a second clutch of eggs, and in one case three clutches. In all, ten clutches were produced that resulted in viable spiderlings. A few females were observed to drop their clutch of eggs briefly and return to it. Four females died in the first two months. It was not until November 2001 that the remaining females were dying regularly. All 22 females were dead by the end of December 2001.

When the eggs are extruded they are ovoid in shape and uniformly translucent. The entire clutch is extruded in a matter of hours, usually during the night. The eggs are more or less arranged in one layer to a pad of silk which the female carries in her chelicerae. For the first 9–11 days the eggs showed no clear sign of development but became more elongate and showed subtle changes in density. Over the next week the leg structure became apparent and development proceeded rapidly with the abdomen and thorax becoming distinct. The developing spiderlings were bunched together with their tarsi connected to the pad of silk. The spiderlings were arranged facing outwards (Fig. 1). Just before leaving the mother, on average three weeks after extrusion, the spiderlings engaged in an activity that we describe as doing 'pushups'. This consisted of actively flexing their legs, which tended to push their body away from the mother and appeared to be associated with the shedding of the first instar exoskeleton. This process was readily observed because at this time females typically positioned themselves upside-down in their webbing. Once they separated from their mother, the spiderlings soon assumed an upside-down orientation in the web. On average, the time between egg production and release of the spiderlings was three weeks to one month. Spiderlings remained in the webbing originally made by the female. The pad of silk containing the remnants of the first instar exuviae remained in the web as well. Within two days after the spiderlings hatched the female moved elsewhere in the dish and established a new web. These relatively dense, irregular sheet webs usually extended from the top of the dish to the side and sometimes to the bottom.

The second instar spiderlings are colorless and virtually transparent. Ten were measured averaging 0.39 mm in body length. Within 2 or 3 days, all but one spiderling produced from each clutch was separated from the mother and placed in separate petri dishes. A few spiderlings were observed attempting to capture smaller springtails. With disappointing regularity the spiderlings disappeared after about 10–14 days whether they were living alone or with the mother. It could not be determined if they had been preyed upon by

Figure 1.—Separately raised *Theotima minutissimus* with clutch of four well developed spiderlings. Spiderlings still attached by legs to a pad of silk carried by the female. The abdomens are directed inward. Space bar = 1 mm.

large springtails. We suspect they died after depleting any energy stores they inherited and/or because they lacked appropriate prey.

In April 2001, four newly hatched spiderlings were transferred into separate petri dishes with soil. Two individuals survived, one for 54 days before it died. The second survived and reached a length of 0.75 mm by January 2002. At this point the spider was judged to be penultimate. On 11 March this spider produced a clutch of four eggs which developed normally. These spiderlings hatched 4 April. The female produced a second clutch of four eggs on 14 April, which developed normally and all four spiderlings became free of the mother (hatched) on 8 May.

While not the first to suggest that some spiders might be parthenogenetic, Machado (1964) extensively examined the possibility for a maleless population of *Theotima* and concluded that the species had to be parthenogenetic. At this time it is not possible to say that the species he studied was or was not conspecific with *Theotima minutissimus*. Lake (1986) reported that a female *Isopeda insignis*, family Heteropodidae, had reproduced parthenogenetically. Gruber (1990), following up an earlier report by Deeleman-Rhinhold (1986) suggesting that *Dysdera hungarica*, family Dysderidae, might be able to reproduce parthenogenetically, kept female *Dysdera hungarica* isolated from males. The females produced egg sacs and a few of the unfertilized eggs ultimately became adults which in turn produced a further generation. Gunnarsson & Andersson (1992) studied chromosome variation in *Pityohyphantes phrygianus*, family Linyphiidae. They discovered that 1–2% of embyros were haploid which suggested development from unfertilized eggs. Shimojana & Nishihira (2000) described a troglodític spider, *Coelotes troglocaecus*, family Amaurobiidae. No males were found and the females had degenerate copulatory organelles.

It would appear that there may be many roads to achieving parthenogenesis in spiders.

Ultimately the question of whether or not an endosymbiotic bacterium such as *Wolbachia* may be involved is worth pursuing now that it has been demonstrated to exist in *Nephila clavata* (Oh et al. 2000). Weeks et al. (2002) caution that there are other endosymbionts or nuclear effects that could be involved. Whatever the case with respect to *Theotima minutissimus*, its world wide distribution and success in its chosen habitat points up the potential evolutionary significance of adopting the parthenogenetic mode of reproduction.

Voucher specimens are deposited in the American Museum of Natural History, New York.

ACKNOWLEDGMENTS

We gratefully acknowledge Kenneth Frank for his many suggestions and comments on the draft manuscript, and subsequently appreciate those of Paula Cushing and Dan Mott. Jill Thompson (El Verde Field Station, Luquillo, Puerto Rico) helped to make life livable in the field. The springtails used to feed the spiders, *Sinella curviseta* Brook (Collembola, Entomobryidae) were from a culture originally provided by Dr. Michael L. Draney, University of Wisconsin-Green Bay.

LITERATURE CITED

Deeleman-Reinhold, C.L. 1986. *Dysdera hungarica* Kulczynski—A case of parthenogenesis? Actas X Congress International Arachnology Jaca (España) 1:25–31.

Deeleman-Reinhold, C.L. 1995. The Ochyroceratidae of the Indo-Pacific Region (Araneae). The Raffles Bulletin of Zoology, Supplement No. 2: 1–103.

Emerit, M. & A. Lopez. 1985. *Ochyrocera thibaudi*, n. sp., et autres Ochyroceratidae des Petites Antilles (Araneae). Revue Arachnologique 6(2): 81–89.

Gruber, J. 1990. Fatherless spiders. British Arachnological Society Newsletter 58:3.

Gunnarsson, B. & A. Andersson. 1992. Chromosome variation in embryos of a solitary spider, *Pityohyphantes phrygianus*, with a skewed sex ratio. Heriditas 117:85–91.

Lake, D.C. 1986. Possible parthenogenesis in the huntsman spider *Isopoda insignis* (Araneae, Sparassidae). Journal Arachnology 14(1):129.

Machado, A.B. 1964. Sur l'existence de la parthénogenese dans quelques espéces d'Araignées Ochyrocératides. Comptes Rendus de L'Academie Science Paris 2(258):5056–5059.

Petrunkevitch, A. 1929. The Spiders of Porto Rico. Transactions Connecticut Academy of Arts & Science, Pt. 1,(30):1–158.

Pfeiffer, W.J. 1996. Litter Invertebrates. Pp. 138–181. *In* The Food Web of a Tropical Rain Forest. (D.P. Reagan, R.B. Waide, Eds.) Univ. Chicago Press.

Platnick, N.I. 1997. Advances in Spider Taxonomy. 1992–1995: With Redescriptions 1940–1980. New York Entomological Society. 976 pp.

Shimojana, M. & M. Nishihira. 2000. A new cave-dwelling eyeless spider of the genus *Coelotes* (Araneae: Amaurobiidae) from Okinawa Island, the Ryukyu Islands, Japan, with notes on possible parthenogenesis. Acta Arachnology 49(1): 29–40.

Oh, H. W., M. G. Kim, S. W. Shin, K. S. Bae & H. Park. 2000. Ultrastructural and molecular identification of a *Wolbachia* endosymbiont in a spider, *Nephila clavata*. Insect Molecular Biology 9:539–543.

Weeks, A.R., K.T. Reynolds & A.A. Hoffmann. 2002. *Wolbachia* dynamics and host effects: what has (and has not) been demonstrated? Trends in Ecology & Evolution 17(6):257–267.

Manuscript received 24 June 2002, revised 15 November 2002.

2003. The Journal of Arachnology 31:278–284

THE EFFECTS OF SIZE, SEX, AND REPRODUCTIVE CONDITION ON THERMAL AND DESICCATION STRESS IN A RIPARIAN SPIDER (*PIRATA SEDENTARIUS*, ARANEAE, LYCOSIDAE)

Jill DeVito[1] and **Daniel R. Formanowicz, Jr.**: Biology Department, Box 19498 University of Texas at Arlington, Arlington, TX 76019. E-mail: devitoj@muohio.edu

ABSTRACT. Within a species, physiological tolerances and thermoregulatory behaviors may vary among ontogenetic stages or between sexes. Such different tolerances can strongly affect the ecology and life history of a species. In a laboratory study, we tested the hypothesis that *Pirata sedentarius* Montgomery 1904 is differentially susceptible to thermal/desiccation stress by size and sex. As predicted, male adults were more susceptible to thermal/desiccation stress than females. Unexpectedly, however, juvenile spiders survived longer under thermal/desiccation stress than adults. Furthermore, female adults without egg sacs displayed a trend toward higher thermal/desiccation tolerance than females carrying egg sacs. These results suggest that for *P. sedentarius*, microhabitat preferences and/or thermoregulatory behaviors may change over the course of development, and may vary between sexes and between females with and without egg sacs.

Keywords: Microhabitat partitioning, ontogenetic changes in physiological tolerances

Lycosid spiders are known to exhibit thermoregulatory behavior to increase their body temperatures above ambient conditions, particularly following a meal or while carrying an egg sac (e.g., Nørgaard 1951; Humphreys 1978), and they can actively regulate evaporative water loss (Aspey et al. 1972). However, they are relatively vulnerable to desiccation (e.g., compared to web-building spiders; Foelix 1996), and water loss is accelerated at higher temperatures (Humphreys 1975).

Previous studies have demonstrated size and sex-related differences in both evaporative water loss and preferred temperatures (Sevacherian & Lowrie 1972; Humphreys 1975; 1978). Male and female spiders often display differential patterns of resource and microhabitat use, as males spend much of their time and energy locating females, and females invest much of their time and energy in egg sac production. Among lycosids, different collecting techniques can yield different sex ratios, and males are reported to travel farther and more often than females (Vlijm & Kessler-Geschiere 1967; Cady 1984). Furthermore, among some lycosids, microhabitat preferences differ between juvenile and adult stages (Vlijm & Kessler-Geschiere 1967; Hallander 1970; Edgar 1971; Kronk & Riechert 1979). Hallander (1970) suggests that this differential microhabitat use may protect juvenile wolf spiders from cannibalism by larger conspecifics.

Pirata sedentarius is a widespread species in North America (Wallace & Exline 1977), but it has, thus far, received very little attention in the literature. In this study, we used *P. sedentarius* (which appears to be a hydrophilic specialist) to test for differences in physiological tolerance to thermal/desiccation stress among ontogenetic stages (size classes), between sexes and between females with and without egg sacs.

METHODS

During the summer of 2001, we sampled two one x five m. plots in the Ten Mile Creek streambed between Lincoln Pond (4 ha) and Lake Myosotis (40 ha), on the Edmund Niles Huyck Preserve and Biological Research Station, Albany County, New York. The creek hydroperiod undergoes seasonal fluctuation

[1] Current address: Department of Zoology, Miami University, Oxford, OH 45056.

and occasional severe flooding; the creek (~2–3 m wide during sampling) occupies a relatively small portion of the streambed, which consists of an extensive un-submerged cobble area under an opening in the forest canopy. Leaf litter and vegetation were absent in the plots sampled during this study, but the cobble is occasionally interspersed with herbaceous vegetation (e.g., the same area during the following summer; DeVito unpubl. data). This habitat is dominated by three lycosid species *Pirata sedentarius*, *Pardosa lapidicina* Emerton 1885, and *Pardosa fuscula* Thorell 1875, and inhabited by at least two others (*Rabidosa* sp. and *Hogna* sp.). The overall abundance of lycosid spiders decreases dramatically outside the streambed (pers. obs.), which is bounded by mixed deciduous leaf litter habitat.

The plots, which represent only the portion of cobble habitat closest to the creek (i.e., ≤ 5 m), were dominated by *P. sedentarius*; only two individual spiders of any other species were found during sampling. Voucher specimens (adult females and males) have been placed in the American Museum of Natural History.

The two plots were laid out perpendicular to the creek (southward from its edge) where the creek bends westward and is crossed by a stepping stone path. Spider collection in Plot 1 was initiated at 1000 h (ambient temperature = 21 °C; partly cloudy; plot shaded throughout; brief light rain) on July 5, and collection in Plot 2 was initiated at 1500 h (ambient temperature = 24 °C; partly cloudy; plot in sun for part of sampling period) on July 6. The plots were partly shaded by canopy cover during both collecting times, and activity of spiders on the rock surfaces was minimal.

One person (JD) sampled the plots, proceeding outward from the creek edge, with the total collecting time for each plot approximating three hours. Every rock in the plot was overturned and each uncovered spider was collected. Soil samples were collected under each rock where a spider was found; these were transported to the laboratory in PVC jars.

To minimize the effects of captivity (e.g., prolonged exposure to artificial moisture levels) spiders and soil samples were processed immediately upon return to the laboratory. Percent soil moisture was estimated for each soil sample using the gravimetric method. Small samples of soil (~ 30–50 g) were weighed, dried in an oven at 40 °C for eight hours, then weighed again. Percent soil moisture was calculated: (dry mass − wet mass)/ wet mass. Mean soil moisture levels were calculated among the samples collected in each square meter of each plot.

Spiders were measured, sexed and divided into the following categories: 1) size class (total body length to the nearest 0.5 mm), 2) sex (juvenile, adult male, or adult female), and 3) reproductive condition (for adult females; egg sac present vs. not present). Spiders were then housed in individual plastic cups covered with fiberglass mesh screen, and placed in a drying oven preheated to 40 °C. This temperature, which probably exceeds the maximal temperatures attained in the streambed (i.e., ~34 °C; DeVito unpubl. data), was tested in preliminary trials because it is standard for drying samples of organic matter over an extended (i.e., eight hour) period. It was ultimately chosen for this study because it was low enough for discrimination among tolerance levels of individual *Pirata sedentarius* but high enough to test the maximal tolerance of *Pardosa lapidicina* and *Pardosa fuscula* within a reasonable (i.e., 14 hour) period.

Time of death was recorded for each spider, rounded up to the nearest ten minutes. Dying spiders assumed a characteristic crenulated posture; death was confirmed by subsequent unresponsiveness to tapping on the container. The tolerance test ended upon the death of the last specimen (290 minutes).

Pearson's correlation was used to test for relationships between soil moisture level, distance from the stream and spider density. Spider survival times at 40 °C were compared between sexes and among size classes using ANOVA (STATISTICA v. 4.5; 1993, Statsoft, Tulsa, OK). We also performed a post-hoc analysis (Chi Square Goodness of Fit Test) of microhabitat use by juvenile size class.

RESULTS

Neither moisture level nor spider density differed between plots (ANOVA; $F_{1,7} = 0.41$; two-tailed $P = 0.54$ for moisture level, and $F_{1,7} = 1.14$; two-tailed $P = 0.32$ for spider density). Data from plots 1 and 2 were therefore pooled for all subsequent analyses.

As expected, mean soil moisture level in

Table 1.—*P. sedentarius* total abundance in streamside plots.

	Distance from stream					
	0–1 m	1–2 m	2–3 m	3–4 m	4–5 m	Total
Small juveniles (2.0–3.0 mm)	9	6	6	5	3	29
Large juveniles (3.5–4.5 mm)	17	10	2	0	2	31
Adult females	7	2	2	3	2	16
Adult males	4	1	1	0	2	8
Total abundance	37	19	11	8	9	84

each (1 m^2) interval decreased with increasing distance from the creek ($r = -0.83$; one-tailed $P < 0.01$; Fig. 1). *Pirata sedentarius* were abundant in the plots (Table 1), and mean spider density was directly related to mean soil moisture level ($r = 0.88$; one-tailed $P < 0.01$) and declined with increasing distance from the creek ($r = -0.7847$; one-tailed $P < 0.01$; Fig. 1).

Survival time (minutes to death at 40 °C) was not normally distributed across the data set (Kolmogorov-Smirnov; d = 0.24; $P < 0.01$). However, after survival time values were log-transformed, the resulting distribution was not significantly different from normal (Kolmogorov-Smirnov; d = 0.10; $P > 0.20$). Log-transformed values were therefore used in all subsequent analyses.

Under the conditions of induced thermal/desiccation stress, juvenile *P. sedentarius* (2.0–4.5 mm) survived longer than adults (ANOVA; $F_{1,75} = 13.1$; $P < 0.001$; Fig. 2). Adult female *P. sedentarius* survived longer than adult males (ANOVA; $F_{1,22} = 37.5$; two-tailed $P < 0.01$), but survival times did not differ between females with and without egg sacs (ANOVA; $F_{1,14} = 3.41$; two-tailed $P = 0.09$). Although adult *P. sedentarius* in this study ranged in size from 4.5–7.0 mm, size had no effect on log survival time while controlling for sex (ANCOVA with sex as covariate; $F_{5,17} = 1.27$; two-tailed $P = 0.32$).

For juvenile *P. sedentarius*, size (TL to the nearest 0.5mm) had a significant effect on log survival time (ANOVA; $F_{5,47} = 6.64$; two-tailed $P < 0.01$). Planned comparisons revealed that small juveniles (2.0–3.0mm) survived longer than large juveniles (3.5–4.5

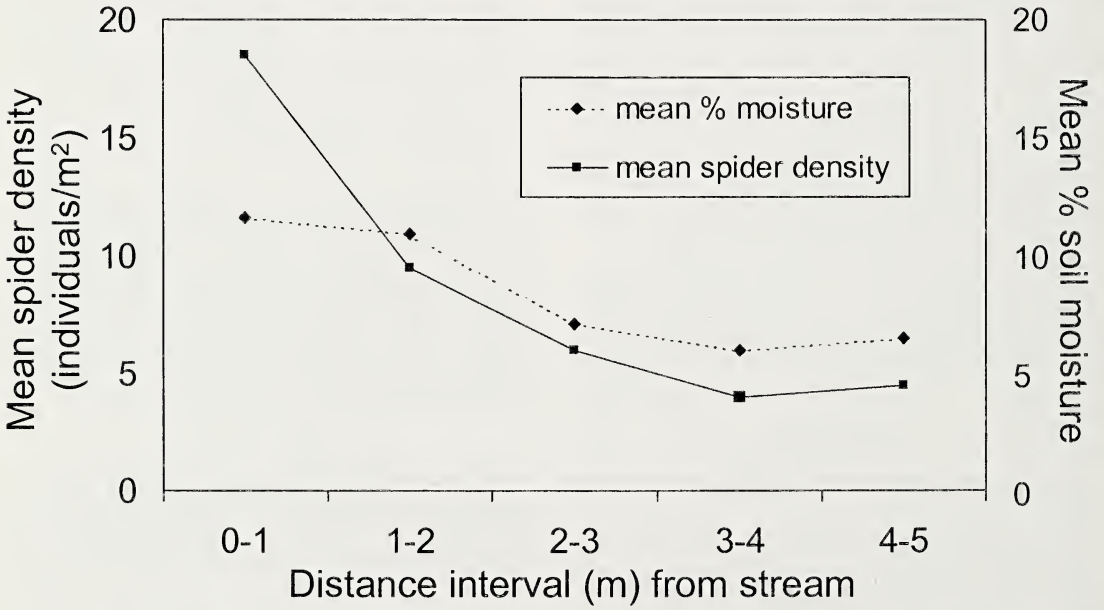


Figure 1.—*Pirata sedentarius* microhabitat use; soil moisture and spider density vs. distance from stream edge.

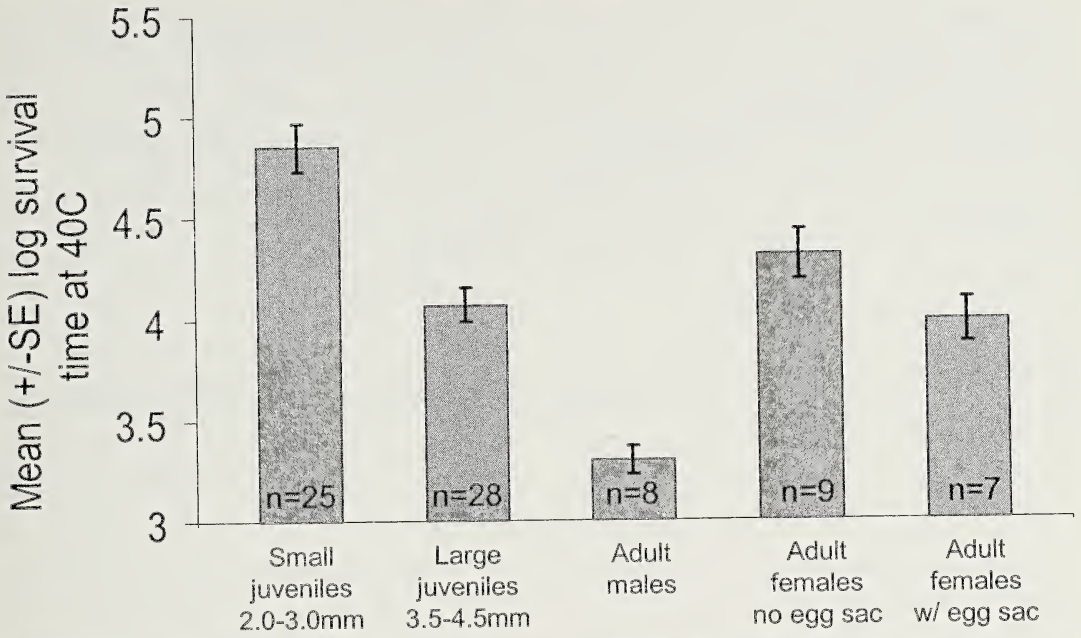


Figure 2.—Effects of size, sex, and reproductive condition on survival time for juvenile and adult *P. sedentarius* under thermal/desiccation stress.

mm) ($F_{1,47}$ = 14.7; two-tailed $P < 0.01$; Fig. 3).

The stress tolerance differences between juvenile size classes prompted us to test the hypothesis that *P. sedentarius* exhibits corresponding ontogenetic changes in microhabitat use. In accordance with this prediction, we found that large juveniles were collected more often than small juveniles in the intervals closer to the creek (X^2_4 = 10.6; P = 0.031; Fig. 4).

DISCUSSION

The high abundance of *P. sedentarius* close to the water is consistent with their relative susceptibility to thermal/dessication stress (e.g., compared to *Pardosa* spp.; DeVito unpubl. data). Furthermore, the streamside habitat may support higher densities of prey items. Humphreys (1975) found that a lycosid spider (*Geolycosa godeffroyi* Koch 1865) was capable of water uptake from a soil substrate with a moisture level above 11%. In our study, the soil moisture levels within the first 2 m of the stream exceed this value.

The differences in thermal/desiccation tolerance found between sexes and among size classes of *P. sedentarius* raised several questions regarding underlying mechanisms and possible ecological significance of the observed effects. The tendency of males to be more prone to thermal/desiccation stress than females is likely related to the considerable difference in body volume (i.e., the volume of the male abdomen being much smaller than the volume of the female abdomen), as large spiders are generally less prone to desiccation than small spiders (Savory 1964). Because male wolf spiders generally travel more widely than females (e.g., Vlijm & Kessler-Geschiere 1967), their increased vulnerability to desiccation is particularly interesting.

The non-significant trend toward higher thermal/desiccation tolerance in females without egg sacs compared to females carrying egg sacs has been confirmed as a significant difference in our more recent study with a larger sample size (DeVito et al. unpubl. data). This finding may reflect a differential ability to withstand physiological stresses based on the amount of energy (i.e., body mass) invested in the egg sac, and resulting differences in abdomen size. Relative thermal/desiccation tolerance may also be influenced by factors such as the time to last feeding, and consequently the size (distention) of the abdomen, and the amount of water currently stored in

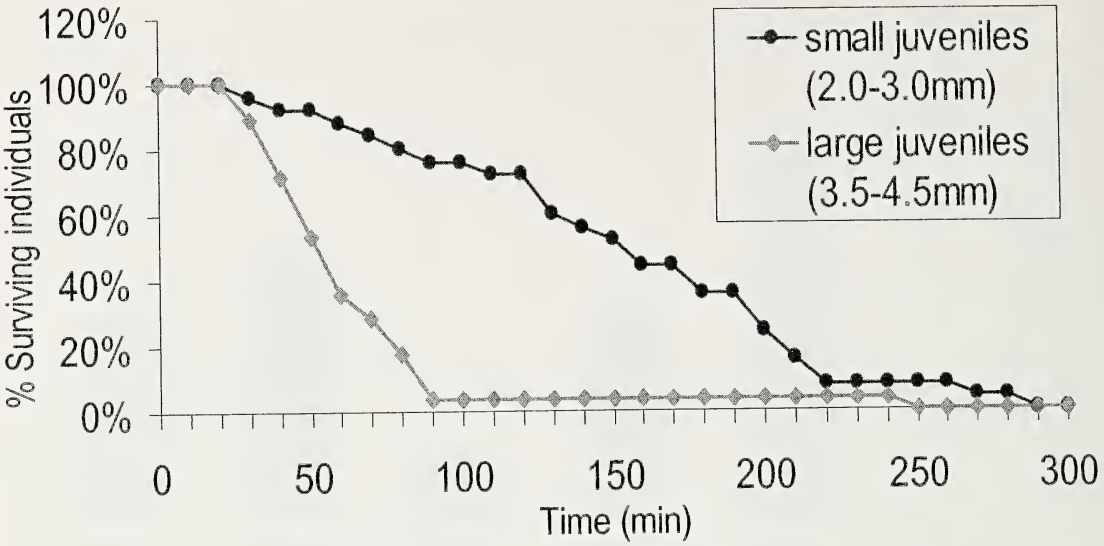


Figure 3.—Survival over time for juvenile *P. sedentarius* size classes under thermal and desiccation stress.

the body. Spiders, which had recently consumed a meal would be predicted to survive longer than hungry spiders under the testing conditions used in this study.

In light of our results, it is surprising that lycosid females (including *P. sedentarius*) carrying egg sacs are more active on sunny days than in overcast conditions (pers. obs.), and that female *Pirata piraticus* Clerck 1757 apparently prefer warmer temperatures when

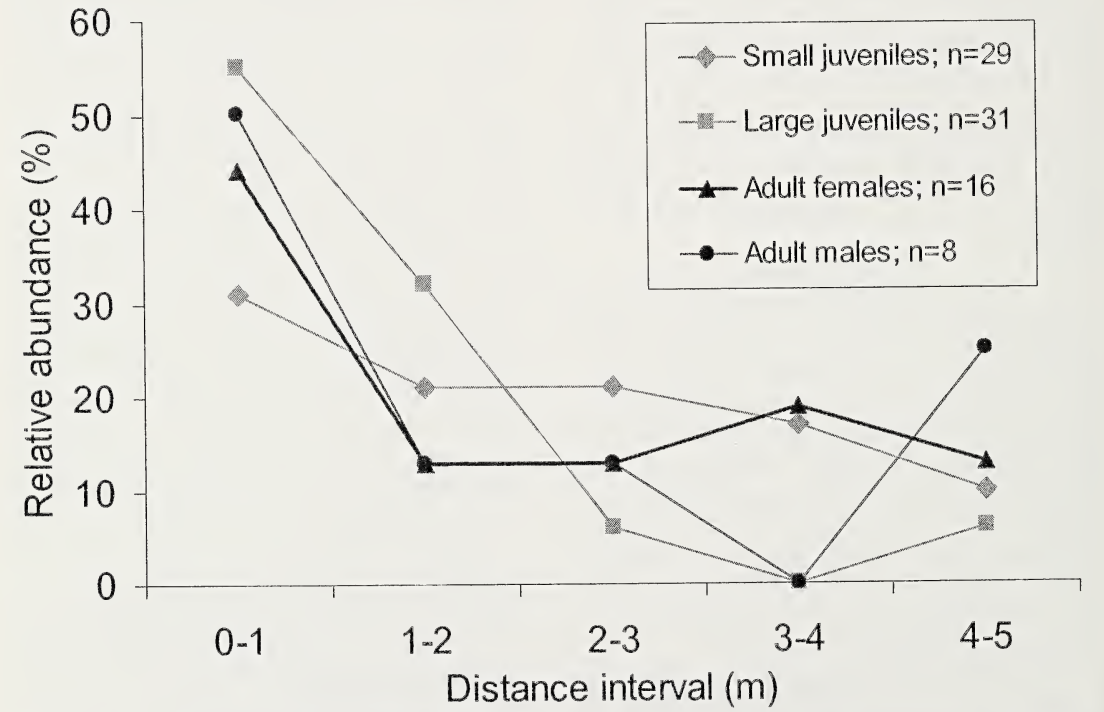


Figure 4.—*P. sedentarius* microhabitat use by sex and size class; proportional abundance vs. distance from stream edge.

they are carrying egg sacs (Nørgaard 1951). Moring and Stewart (1994) also found that spiders (*Pardosa* and *Alopecosa* species) in a streamside cobble habitat in Colorado were more active as light intensity increased.

It seems likely that female lycosids with egg sacs walk a fine line between keeping egg sacs warm enough and protecting themselves from thermal/desiccation stress. The proximity of refugia (e.g., moist soil conditions in cobble habitats) probably plays a very large role in habitat use for streamside lycosid spiders in general. Females carrying egg sacs may further require heterogeneous climatic conditions (e.g., exposed rock surfaces in cobble habitats) to balance the thermal requirements of the egg sac with their own physiological limitations.

Given the general tendency of larger spiders to be less vulnerable to desiccation than smaller spiders (along with the fact that desiccation is accelerated at higher temperatures), the finding that juvenile *P. sedentarius* survive much longer than adults was surprising. This result is not consistent, for example, with the results of Sevacherian & Lowrie (1972), who found that juveniles of two *Pardosa* species preferred lower temperatures than adults.

We speculate that the higher thermal/desiccation tolerance of (especially the smallest) juvenile size classes might be due to the storage of lipids from the yolk sac. Furthermore, the extremely high tolerances of a few individual juveniles may have resulted from individual variation in the timing of molt cycles. Spiders approaching a new molt cycle would have two layers of cuticle, perhaps affording more protection from desiccation, in comparison with spiders that had recently molted. The ontogenetic differences in thermal/desiccation tolerance and microhabitat use observed in this study lead to the implication that small juvenile *P. sedentarius* can tolerate warm, dry conditions more successfully than large juveniles and adults. Such an adaptation would facilitate dispersal from the back of the mother. This possibility is reflected by the parallel habitat use of small juveniles and adult females (Fig. 4).

The tendency of large juveniles to be concentrated at the edge of the water is consistent with their reduced thermal/desiccation tolerance compared to small juveniles. However, if food resources are more abundant closer to the stream, this pattern may alternatively reflect the exploitation of those resources by spiders which 1) can no longer rely on the yolk sac and 2) do not yet need to warm an egg sac or wander in search of females. Future studies should explore the possibility of differential thermoregulatory behavior among size classes, as well as ontogenetic changes in microhabitat use.

ACKNOWLEDGMENTS

This study was conducted with the assistance of a research grant from the E.N. Huyck Preserve & Biological Research Station. This foundation also provided access to equipment and supplies. Additional funding was provided by the University of Texas at Arlington Biology Department. J. McGuinness instructed J. DeVito in the use of equipment and contributed ideas to the experimental design. S. Beatty instructed J. DeVito in the gravimetric method of measuring soil moisture. C. Amaya and M. Pfeiffer contributed to the interpretation of our results. C. Brown, M. Gerson, M. Nelson and M. Pfeiffer provided critical reviews of an earlier version of this manuscript. P.E. Cushing, M.C. Lowder, D. Mott, G. Stratton, and an anonymous reviewer offered helpful comments during the review process.

LITERATURE CITED

Aspey, W.P., C. Lent & M. Meeker. 1972. Effect of humidity on desiccation by living and dead wolf spiders (Araneae, Lycosidae). Experientia 28: 1249–1250.

Cady, A.B. 1984. Microhabitat selection and locomotor activity of *Schizocosa ocreata* (Walckenaer) (Araneae, Lycosidae). Journal of Arachnology 11:297–307.

Edgar, W.D. 1971. The life-cycle, abundance and seasonal movement of the wolf spider, *Lycosa* (*Pardosa*) *lugubris*, in central Scotland. Journal of Animal Ecology 40:303–322.

Foelix, R.F. 1996. Biology of Spiders. Oxford University Press, New York.

Hallander, H. 1970. Prey, cannibalism and microhabitat selection in the wolf spiders *Pardosa chelata* O.F. Müller and *P. pullata* Clerck. Oikos 21: 337–340.

Humphreys, W.F. 1975. The influence of burrowing and thermoregulatory behaviour on the water relations of *Geolycosa godeffroyi* (Araneae: Lycosidae), an Australian wolf spider. Oecologia 21:291–311.

Humphreys, W.F. 1978. The thermal biology of *Geolycosa godeffroyi* and other burrow inhabit-

ing Lycosidae (Araneae) in Australia. Oecologia 31:319–347.

Kronk, A.W. & S.E. Riechert. 1979. Parameters affecting the habitat choice of *Lycosa santrita* Chamberlin and Ivie. Journal of Arachnology 7: 155–166.

Moring, J.B. & K.W. Stewart. 1994. Habitat partitioning by the wolf spider (Araneae, Lycosidae) guild in streamside and riparian vegetation zones of the Conejos River, Colorado. Journal of Arachnology 22:205–217.

Nørgaard, E. 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. Oikos 3:1–21.

Savory, T. 1964. Arachnida. Academic Press. London.

Sevacherian, V. & D.C. Lowrie. 1972. Preferred temperatures of two species of lycosid spiders, *Pardosa sierra* and *P. ramulosa*. Annals of the Entomological Society of America 65:111–114.

Vlijm, L. & A.M. Kessler-Geschiere. 1967. The phenology and habitat of *Pardosa monticola*, *P. nigriceps* and *P. pullata* (Araneae, Lycosidae). Journal of Animal Ecology 36:31–56.

Wallace, H.K. & H. Exline. 1977. Spiders of the genus *Pirata* in North America, Central America, and the West Indies (Araneae, Lycosidae). Journal of Arachnology 5:1–112.

Manuscript received 22 April 2002, revised 11 December 2002.

2003. The Journal of Arachnology 31:285–296

CLUTCH SIZE AND OFFSPRING SIZE IN THE WOLF SPIDER *PIRATA SEDENTARIUS* (ARANEAE, LYCOSIDAE)

Christopher A. Brown,[1] **Bridget M. Sanford** and **Rebekah R. Swerdon**: Dept. of Biology, State University of New York College at Fredonia, Fredonia, New York 14063 USA

ABSTRACT. Wolf spiders in the genus *Pirata* are common, often locally abundant, inhabitants of many moist or mesic habitats. However, relatively little is known about the ecology or life history of these spiders. Here we present data collected during 2000–2001 on female size, offspring size and clutch size for two populations (Ball Gulf, Hardscrabble Creek) of *Pirata sedentarius* from western New York. In both populations, mean offspring size was less variable than was female size, clutch size or total clutch mass. At Ball Gulf, 67% of females produced two egg sacs and 48% produced three sacs. Clutch size declined across the egg sac sequence for all females. Female size, measured as cephalothorax length, was uncorrelated with mean offspring size in all cases. However, larger females produced larger and heavier clutches during 2001 for both populations; female size was uncorrelated with these variables during 2000 at Hardscrabble Creek. Larger clutches from both populations contained more offspring, and larger clutches contained smaller offspring at Hardscrabble Creek in 2001. We found a significant offspring size-number trade-off at Ball Gulf, while at Hardscrabble Creek this trade-off was marginally significant in 2001 and non-significant in 2000.

Keywords: Lycosidae, *Pirata*, life history, clutch size, offspring size

The interrelationships among clutch size, offspring size, and female size have been the subject of much empirical and theoretical research, due to the influence of these life history traits on both offspring and parental fitness (see reviews in Clutton-Brock 1991; Roff 1992, 2002; Stearns 1992; Bernardo 1996). Two general results have emerged from this work. The first is the empirical observation that larger females typically produce more and, somewhat less commonly, larger offspring (Roff 1992, 2002; Stearns 1992). The simplest explanation for these relationships is that larger females have more available space in which to store developing offspring (eggs or embryos), although other factors (such as size-based differences in resource usage; see below) may also have an effect.

The second result is the theoretical prediction that clutch size and offspring size should exhibit a trade-off (Smith & Fretwell 1974; Roff 1992, 2002; Stearns 1992). Such a trade-off should exist within individuals because given finite resources for reproduction, females choosing to make larger offspring must necessarily make fewer of them. Empirical evidence for this trade-off has been mixed (see reviews in Roff 1992; Stearns 1992). While many species do exhibit a size-number trade-off, others do not, and the magnitude and direction of the trade-off may vary among populations or among years within a population (e.g., Brown 2001). The lack of a trade-off may be explained by differences among females in their access to resources, such that females of high quality may make both more and larger offspring that low quality females (van Noordwijk & de Jong 1986; Flint et al. 1996; Christians 2000). Thus, female size potentially affects offspring size and number in two ways. Larger females may have more room in which to carry developing offspring, and they may be better able to obtain, defend, store, or allocate (to reproduction) resources.

For spiders, relationships among clutch size, offspring size, and female size have been examined using both inter- and intraspecific data. In comparative studies across species,

[1] Current address: Department of Biology, Box 5063, Tennessee Technological University, Cookeville, TN 38505. E-mail: cabrown@tntech.edu.

female size has been shown to correlate positively with clutch size and/or offspring size (Petersen 1950; Enders 1976; Marshall & Gittleman 1994; Simpson 1995; Prenter et al. 1999), while a size-number trade-off has been found in one study (Simpson 1995) but not another (Marshall & Gittleman 1994). Clutch size also generally increases with female size within a single species (e.g., Briceño 1987; McLay & Hayward 1987; Vollrath 1987; Morse 1988; Tanaka 1992; Simpson 1993; Punzo & Henderson 1999; Buddle 2000), while offspring size may increase with (e.g., Tanaka 1995) or be unrelated to (e.g., Kessler 1971) female size. Intraspecific studies have also found evidence for (Simpson 1993; Tanaka 1995) and against (Simpson 1993) the existence of an offspring size-number trade-off.

Wolf spiders of the genus *Pirata* Sundevall 1833 occur worldwide, predominantly in moist areas such as swamps, bogs, damp forests or meadows and along the shores of ponds or streams. In these habitats they may be one of the most abundant groups of wandering spiders (Nørgaard 1951; Wallace & Exline 1978). Since *Pirata* can easily move on the water as well as on land, they are potentially important conduits of energy and nutrients between aquatic and terrestrial ecosystems. However, their ecology and life histories have received scant attention, particularly among New World species. In this study we report data on clutch size, offspring size, and female size for two populations of the wolf spider *Pirata sedentarius* Montgomery 1904, a widely distributed species found throughout North America and the West Indies (Dondale & Redner 1990). For one population, we also examine changes in clutch size over the breeding season. This represents one of the few studies in which the relationships between these three life history traits have been studied simultaneously within a single species of spider.

METHODS

We collected *P. sedentarius* females from two locations in western New York. In this area, *P. sedentarius* occurs most commonly in the moist cobble zone along creek banks. The first site was an unnamed creek near the intersection of Creamery Road and Hardscrabble Road, approximately 4.7 km west of Westfield, New York (henceforth the Hardscrabble Creek population). Females were collected here on 21 July 2000 (n = 17) and on 22 May (n = 1) and 17 July 2001 (n = 17). The second site, approximately 33 km ENE of Hardscrabble Creek, was a small tributary of Canadaway Creek running through Ball Gulf in the town of Arkwright, New York (henceforth the Ball Gulf population). Females were collected here from 14–27 June 2001 (n = 21). All females were gravid or carrying egg sacs, with the exception of two females from Hardscrabble Creek in 2000 carrying second instar offspring. Gravid females produced an egg sac within seven days of capture, so that effects of captivity (such as changes in food availability) on reproduction should be negligible.

On return to the laboratory, each female was housed individually in a 0.95 L translucent plastic container, fitted with a lid perforated several times to provide air holes. The bottom of the container was lined with a piece of paper toweling which was kept moistened. Females in 2000 also had access to water ad libitum via a one dram shell vial stoppered with a cotton ball. Females were offered 1–2 two-week-old crickets every 5–7 days.

Containers were checked daily for the presence of spiderlings on the female's back or for dispersed spiderlings. For the latter, we considered a clutch to have dispersed if > 50% (by visual inspection) of the offspring were off the female's back. Following dispersal, we weighed each female to the nearest one mg. All live spiderlings in a clutch were weighed together to obtain the total clutch mass (TCM), again to the nearest one mg; we determined mean offspring mass by dividing TCM by clutch size (which included dead spiderlings). After masses were obtained we immediately preserved all spiderlings, living or dead, in 70% ethanol. From each preserved clutch we determined clutch size and, for the 2000 Hardscrabble Creek population only, measured the cephalothorax length (CL, in mm) of 10 randomly selected spiderlings using an Olympus SZ40 dissecting microscope fitted with an optical micrometer. As a measure of investment in reproduction relative to female size, we also calculated relative clutch mass by dividing TCM by female mass.

Because females were being used in an experiment (see below), only seven of the clutches from Hardscrabble Creek in 2001

were allowed to hatch. For the remainder, egg sacs were gently removed from the female using forceps and preserved in 70% ethanol. Clutch size was subsequently determined by counting eggs or larvae.

Females were preserved in 70% ethanol either immediately after offspring dispersal (in 2000) or after being used in a series of trials examining the effect of leg loss on sprint speed (in 2001; P. Apontes & C. Brown, unpub. data). After preservation, female CL was measured (in mm) on a Meiji RZ dissecting microscope equipped with an optical micrometer. Between dispersal of the first clutch and female preservation, many of the Ball Gulf spiders produced a second, and in some cases a third, egg sac. These sacs were removed from the female as produced and preserved in 70% ethanol. Clutch size was then determined by counting eggs. Voucher specimens from each population have been deposited in the American Museum of Natural History, New York.

We examined relationships among the various life history traits using correlation analysis (Pearson's r) or least-squares regression on log-transformed data. The trade-off between offspring size and number was examined by first regressing clutch size and offspring size separately against female size, and then using residuals from these regressions in a correlation analysis. This procedure statistically controls for variation in these traits due to female size. Finally, comparisons of life history variables between years or populations were done by ANOVA on log-transformed data, with the exception of relative clutch mass, which was untransformed. All analyses were done using Statistica for Windows version 4.5 (StatSoft 1993).

RESULTS

A summary of the life history data for the two populations of *P. sedentarius* is presented in Table 1. Most variables exhibited substantial variation, with coefficients of variation (CVs) usually above 20%. The primary exceptions were offspring CL and female CL, which had CVs <10%. Mean offspring mass varied less than did female mass, clutch size, total clutch mass (TCM), or relative clutch mass for both populations. Hardscrabble Creek did not differ between years in female mass ($F_{1,22} = 0.44$, $P = 0.52$), female CL ($F_{1,31} = 2.46$, $P = 0.13$), mean offspring mass ($F_{1,21} = 2.84$, $P = 0.11$), clutch size ($F_{1,32} = 0.001$, $P = 0.97$), TCM ($F_{1,21} = 0.22$, $P = 0.64$), or relative clutch mass ($F_{1,21} = 0.59$, $P = 0.45$). Therefore, data for this population were combined for all subsequent ANOVAs.

Of the 21 Ball Gulf females which produced an initial egg sac, 14 produced a second sac and 10 a third sac. The second egg sac was produced one month (range 31–34 days) after the first sac, and the third sac occurred 2–4 weeks after the second sac (range 14–28 days). For all females clutch size declined in each successive egg sac (Table 1; Fig. 3). However, clutch size was strongly positively correlated across sacs (sac 1 vs. sac 2: $r = 0.87$, $P < 0.001$, $n = 14$; sac 1 vs. sac 3: $r = 0.86$, $P = 0.001$, $n = 10$; sac 2 vs. sac 3: $r = 0.81$, $P = 0.004$, $n = 10$). Comparing first clutches laid in the laboratory indicated that Ball Gulf females produced significantly larger clutches than did Hardscrabble Creek females ($F_{1,53} = 7.11$, $P = 0.01$). However, clutches laid at the same time (Hardscrabble Creek first clutches and Ball Gulf second clutches) were not significantly different in size ($F_{1,46} = 1.02$, $P = 0.32$). Thus, results for Hardscrabble Creek may represent either production of a smaller first clutch or production of a similarly-sized second clutch as compared to Ball Gulf. The latter result seems more likely, given that at least one Hardscrabble Creek female produced an egg sac by late May.

Females from Hardscrabble Creek were larger than their counterparts from Ball Gulf, although this result is only marginally significant for both mass ($F_{1,40} = 3.63$, $P = 0.06$) and CL ($F_{1,52} = 3.77$, $P = 0.06$). However, mean offspring mass did not differ between populations ($F_{1,39} = 0.46$, $P = 0.50$). Total clutch mass ($F_{1,39} = 4.73$, $P = 0.04$) and relative clutch mass ($F_{1,39} = 11.5$, $P = 0.002$) were both significantly higher at Ball Gulf, reflecting the greater clutch sizes in this population.

Female mass and CL were significantly positively correlated in both populations (2000 Hardscrabble Creek: $r = 0.80$, $P < 0.001$, $n = 16$; 2001 Hardscrabble Creek: $r = 0.97$, $P = 0.002$, $n = 6$; 2001 Ball Gulf: $r = 0.79$, $P < 0.001$, $n = 18$). Therefore, we used female CL as our measure of size in the following analyses; using mass gives qualitatively similar results. Since offspring were weighed in both years, we used mass as our

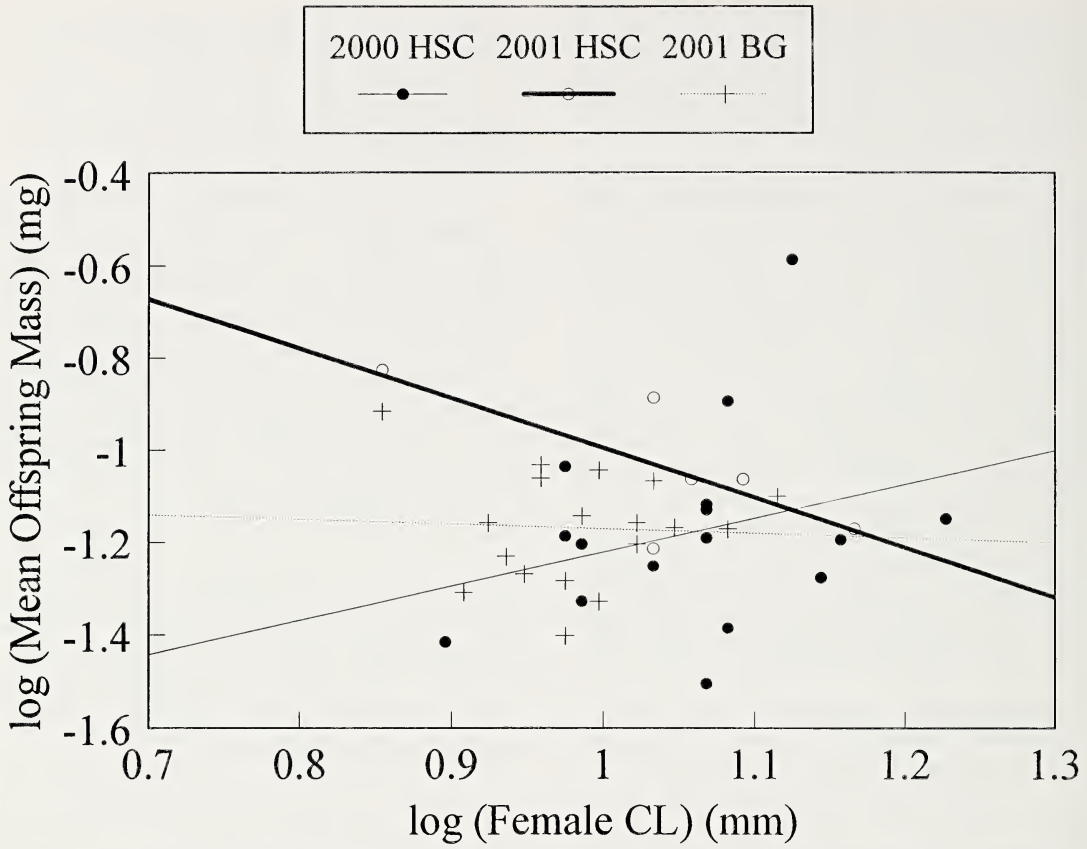


Figure 1.—Linear regressions of mean offspring mass (MOM) against female carapace length (FCL; both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Regression equations: 2000 Hardscrabble Creek: MOM = −1.96 + 0.74*FCL, $F_{1,14}$ = 1.20, P = 0.29, R^2 = 0.08; 2001 Hardscrabble Creek: MOM = 0.09 - 1.08*FCL, $F_{1,4}$ = 4.52, P = 0.10, R^2 = 0.53; Ball Gulf: MOM = −1.08 - 0.09*FCL, $F_{1,16}$ = 0.04, P = 0.85, R^2 = 0.002.

measure of offspring size. Using offspring CL gave qualitatively similar results for the 2000 Hardscrabble Creek population, as mass and CL were significantly positively correlated (r = 0.61, P = 0.012, n = 16). Female size was uncorrelated with mean offspring size in both populations and years (Fig. 1). Female size was also uncorrelated with clutch size during 2000 at Hardscrabble Creek (Fig. 2). However, larger females produced larger clutches at Hardscrabble Creek in 2001, and larger first, second, and third clutches at Ball Gulf (Figs. 2, 3). Larger females produced heavier clutches in both populations during 2001, while female size was unrelated to TCM in 2000 (Fig. 4).

Heavier litters contained more offspring in all populations and years (Fig. 5). The relationship between TCM and offspring size was more complex (Fig. 6). These two variables were uncorrelated for the Ball Gulf and 2000 Hardscrabble Creek populations, while in 2001 at Hardscrabble Creek heavier litters contained smaller offspring. We found a negative relationship between offspring size and number in all population-year combinations (Fig. 7). This trade-off was not significant at Hardscrabble Creek in 2001 (r = −0.46, P = 0.36, n = 6), perhaps due to the low sample size. However, there was a significant size-number trade-off at Ball Gulf (r = −0.65, P = 0.003, n = 18) and a marginally significant trade-off at Hardscrabble Creek in 2000 (r = −0.50, P = 0.06, n = 16).

DISCUSSION

Our results indicate that *P. sedentarius* females in western New York are capable of

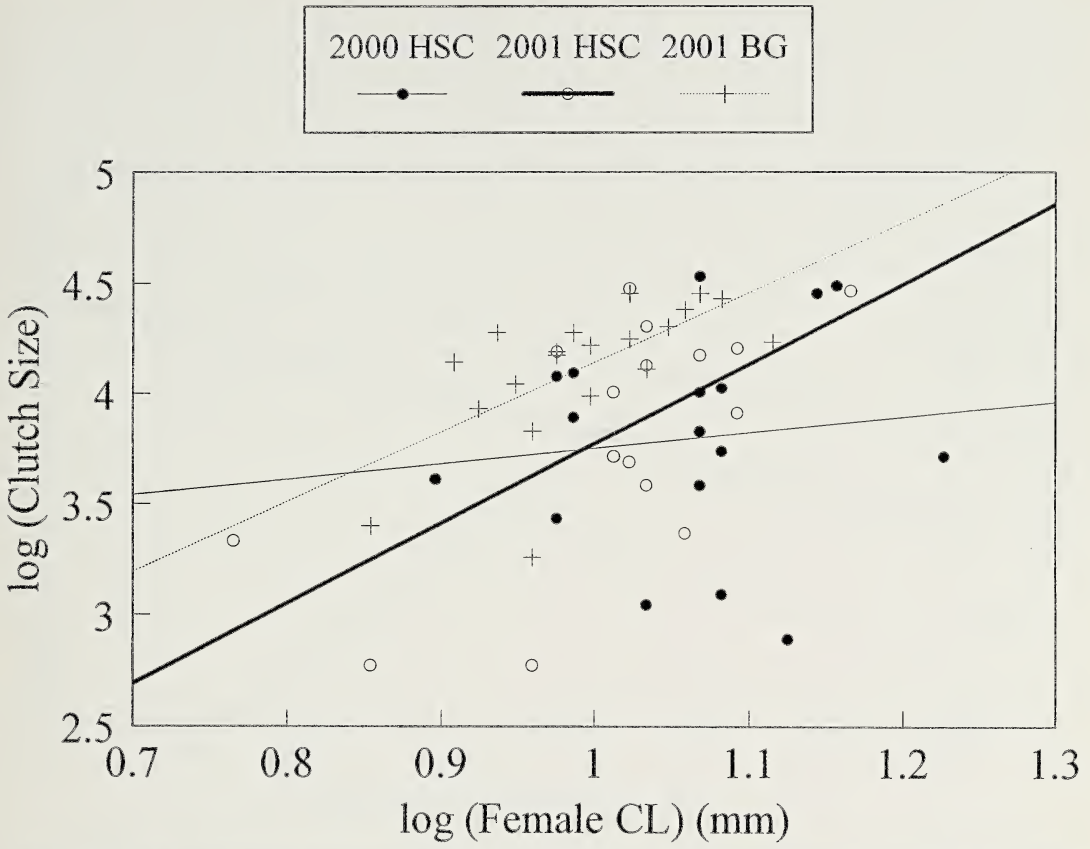


Figure 2.—Linear regressions of initial clutch size (CS) against female carapace length (FCL; both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Regression equations: 2000 Hardscrabble Creek: CS = 3.05 + 0.70*FCL, $F_{1,15} = 0.20$, $P = 0.66$, $R^2 = 0.01$; 2001 Hardscrabble Creek: CS = 0.16 + 3.61*FCL, $F_{1,14} = 9.29$, $P = 0.009$, $R^2 = 0.36$; Ball Gulf: CS = 0.98 + 3.16*FCL, $F_{1,19} = 12.9$, $P = 0.002$, $R^2 = 0.41$.

Table 1.—Summary life history data [mean ± SD (coefficient of variation)] for *Pirata sedentarius*. An unmeasured variable is indicated by NA. CL = cephalothorax length. *Number of litters and females weighed/total number of litters and females measured.

	Hardscrabble Creek		Ball Gulf
	2000	2001	2001
Female mass (mg)	24.1 ± 7.7 (31.8)	29.3 ± 7.2 (24.7)	21.8 ± 4.9 (22.4)
Female CL (mm)	2.90 ± 0.23 (8.0)	2.76 ± 0.30 (9.6)	2.71 ± 0.17 (6.2)
Offspring Mass (mg)	0.32 ± 0.08 (24.8)	0.36 ± 0.05 (14.4)	0.31 ± 0.04 (12.3)
Offspring CL (mm)	0.8 ± 0.05 (6.9)	NA	NA
Clutch Size 1	49.5 ± 22.9 (46.4)	50.2 ± 22.6 (45.1)	64.2 ± 16.1 (25.1)
Clutch Size 2	NA	NA	40.5 ± 12.5 (30.8)
Clutch Size 3	NA	NA	24.8 ± 7.6 (30.5)
Total Clutch Mass (mg)	15.1 ± 6.9 (46.1)	16.7 ± 7.4 (44.5)	19.0 ± 4.6 (24.2)
Relative Clutch Mass	0.66 ± 0.30 (45.1)	0.57 ± 0.21 (37.4)	0.88 ± 0.15 (17.1)
Sample Size	17	7/17*	21

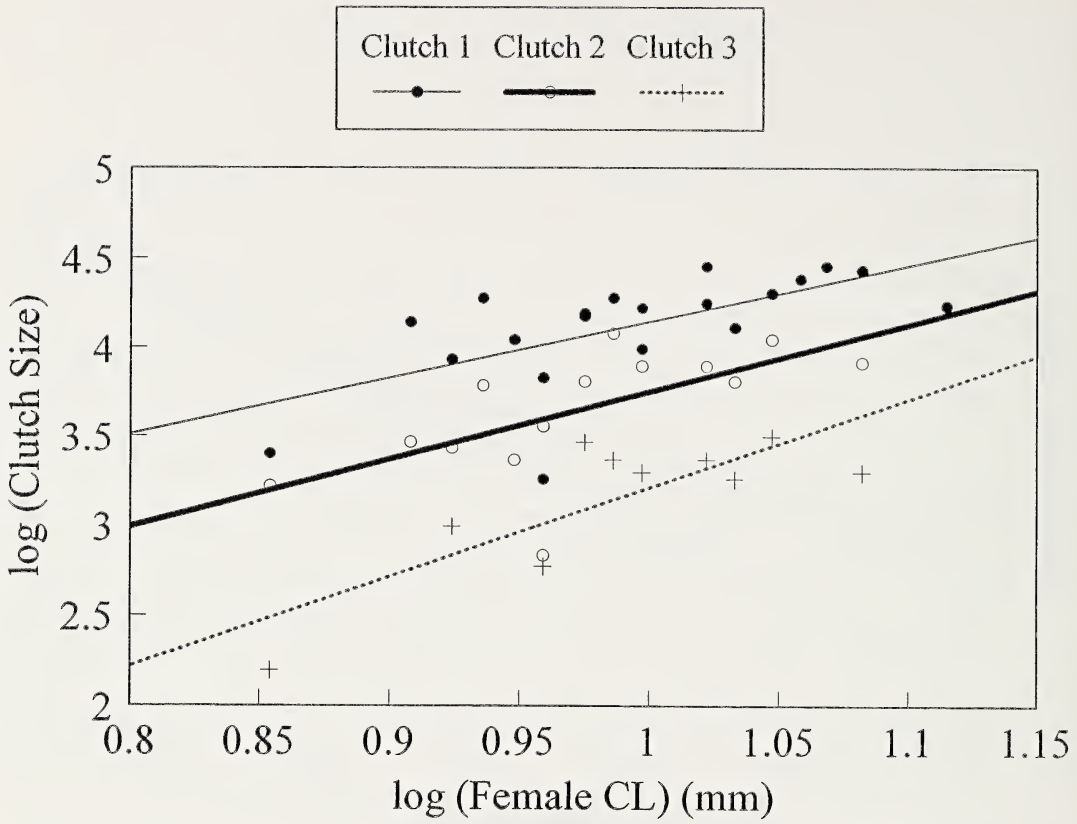


Figure 3.—Linear regressions of clutch size (CS) against female carapace length (FCL; both log transformed) for the first through third egg sacs produced by *Pirata sedentarius* females at Ball Gulf. Regression equations: first clutch: CS = 0.98 + 3.16*FCL, $F_{1,19}$ = 12.9, P = 0.002, R^2 = 0.41; second clutch: CS = −0.04 + 3.79*FCL, $F_{1,12}$ = 8.71, P = 0.01, R^2 = 0.42; third clutch: CS = −1.75 + 4.96*FCL, $F_{1,8}$ = 15.32, P = 0.004, R^2 = 0.66.

producing multiple egg sacs over the course of the breeding season. Whitcomb (1967, cited in Marshall & Gittleman 1994) has also shown that *P. sedentarius* can produce multiple egg sacs, on average 2.5/yr (compared to 2.1 in the present study). We have observed egg sacs in the field as early as mid May and as late as early September in our study populations as well as other populations in western New York. Based on this, we expect that most or all of the initial Ball Gulf sacs produced in the laboratory represent first clutches, while the Hardscrabble Creek sacs are either all second clutches or a mixture of first and second clutches.

While the interclutch interval between sacs one and two (one month) may reasonably approximate natural events, it seems likely to us that the interval between sacs two and three (a minimum of two weeks) was shortened in at least some spiders. For first sacs produced in the laboratory, the time until hatching ranged from 17–23 days, and offspring were carried for an additional 2–5 days. Thus, unless offspring develop substantially faster in second than in first clutches, our removal of the egg sac led some females to speed up production of the next clutch. Females that lose an egg sac early enough in the breeding season may still then have the ability to produce three (or more) clutches, albeit at the cost of a reduction in overall fecundity.

Mean clutch size for both populations falls within the range (19–93.7) given by Kaston (1946) for five species of *Pirata*. Ball Gulf first clutches are similar in size to the mean values of 63.8 and 54.0 reported for *P. sedentarius* by, respectively, Kaston (1946, under the name *P. maculatus*) and Whitcomb (1967, cited in Marshall & Gittleman 1994). As has

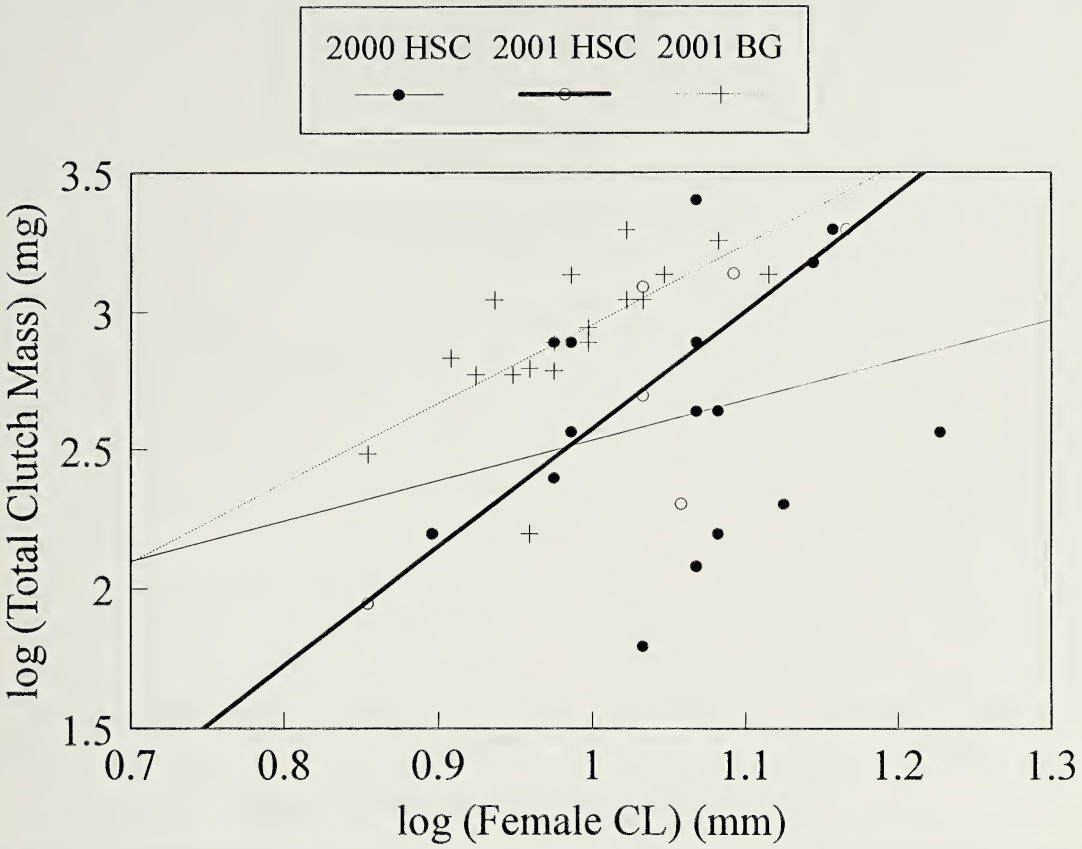


Figure 4.—Linear regressions of total clutch mass (TCM) against female carapace length (FCL; both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Regression equations: 2000 Hardscrabble Creek: TCM = 1.08 + 1.45*FCL, $F_{1,14} = 1.06$, $P = 0.32$, $R^2 = 0.07$; 2001 Hardscrabble Creek: TCM = −1.69 + 4.27*FCL, $F_{1,4} = 8.88$, $P = 0.04$, $R^2 = 0.69$; Ball Gulf: TCM = 0.08 + 2.88*FCL, $F_{1,16} = 13.2$, $P = 0.002$, $R^2 = 0.45$.

been found in a number of other temperate-zone animals (e.g., lizards: Ferguson & Bohlen 1978; birds: Lack 1968; spiders: Foelix 1996), offspring/egg numbers decline over the course of the breeding season (but see Eberhard 1979 for a counterexample in tropical spiders). This decline may be due to a decrease in the amount of resources available to the female for making eggs, or may represent an adaptive shift to the production of fewer, larger offspring which have an increased survival rate when born later in the year (Nussbaum 1981; Ferguson et al. 1982; Roff 1992). Our result showing that Hardscrabble Creek offspring (presumably second clutches) were similar in size to Ball Gulf offspring (first clutches) makes the latter explanation seem less likely for *P. sedentarius*, although this assumes that Hardscrabble Creek first clutches will also have offspring of similar size. We currently lack sufficient data to address this assumption.

Literature reports of offspring size in *Pirata* are uncommon, but newly emerged spiderlings (as well as adults) of *P. sedentarius* are larger than the corresponding life stage of *P. piraticus* (Clerck 1758) (Yu et al. 2001). Relative clutch mass in *P. sedentarius* was higher than the mean value of 0.5 calculated for 14 species from Table 2 of Marshall & Gittleman (1994), although lower than in several other wandering spiders [e.g., the oxyopid *Peucetia viridans* (Hentz 1832) (Killebrew & Ford 1985); the lycosid *Pardosa lugubris* (Walckenaer 1802) (Edgar 1971)].

During 2001, larger females from both populations produced larger (first, second, and third) clutches, the typical pattern found in

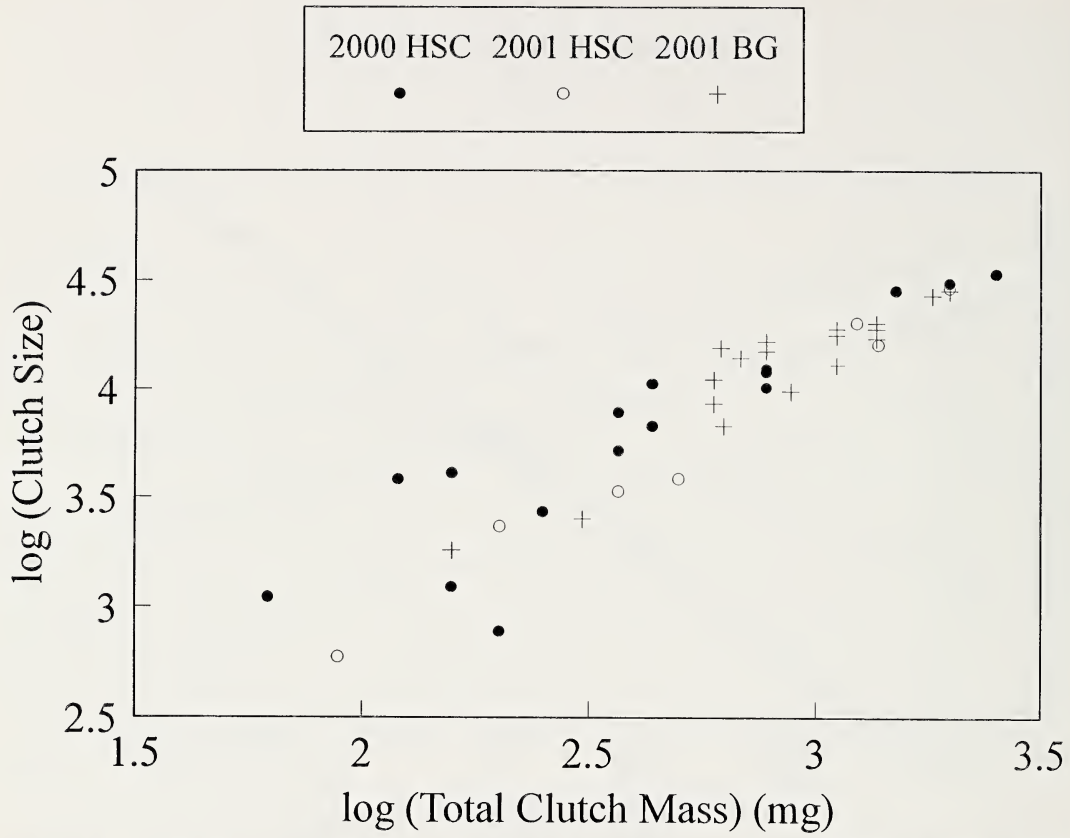


Figure 5.—Correlations between total clutch mass and clutch size (both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Correlations: 2000 Hardscrabble Creek: $r = 0.90$, $P < 0.001$, $n = 16$; 2001 Hardscrabble Creek: $r = 0.99$, $P < 0.001$, $n = 7$; Ball Gulf: $r = 0.93$, $P < 0.001$, $n = 18$.

most invertebrates (reviews in Roff 1992; Stearns 1992), including lycosid (e.g., Petersen 1950; Kessler 1971) and non-lycosid (e.g., Harrington 1978; Austin 1984; Fritz & Morse 1985; Killebrew & Ford 1985; McLay & Hayward 1987; Suter 1990; Punzo & Henderson 1999) spiders. In fact, female size accounted for 36–66% of the variation observed in offspring number during 2001. Larger females also produced heavier clutches in both populations during 2001. The lack of a significant effect of female size on clutch size or mass at Hardscrabble Creek in 2000 was therefore surprising, particularly given that neither female size, clutch size nor TCM varied between years in this population. An examination of the regression equations (Fig. 2) shows that relatively small females produced larger, heavier clutches in 2000 than in 2001, while relatively large females produced larger, heavier clutches in 2001. This suggests that resources available to females differed among years, and only smaller females were in good enough condition (i.e., obtained enough resources) during 2000 to produce a normal clutch for their size. Differences in residual condition indices (residuals from the regression of female mass on CL; Jakob et al. 1996) were in the predicted direction (2001: mean ± SD = 0.26 ± 0.24; 2000: mean ± SD = −0.09 ± 1.12), although the lack of significance ($F_{1, 21} = 0.57$, $P = 0.46$) indicates at best weak support for this hypothesis.

Contrary to the results for clutch size, female size was unrelated to offspring size in either population. This appears to be a common result in spiders (e.g., Kessler 1971; McLay & Hayward 1987; Killebrew & Ford 1985) and other arachnids (Brown 2001), although a number of other invertebrate taxa do exhibit an increase in offspring size with female size (reviewed in Roff 1992). Recalling

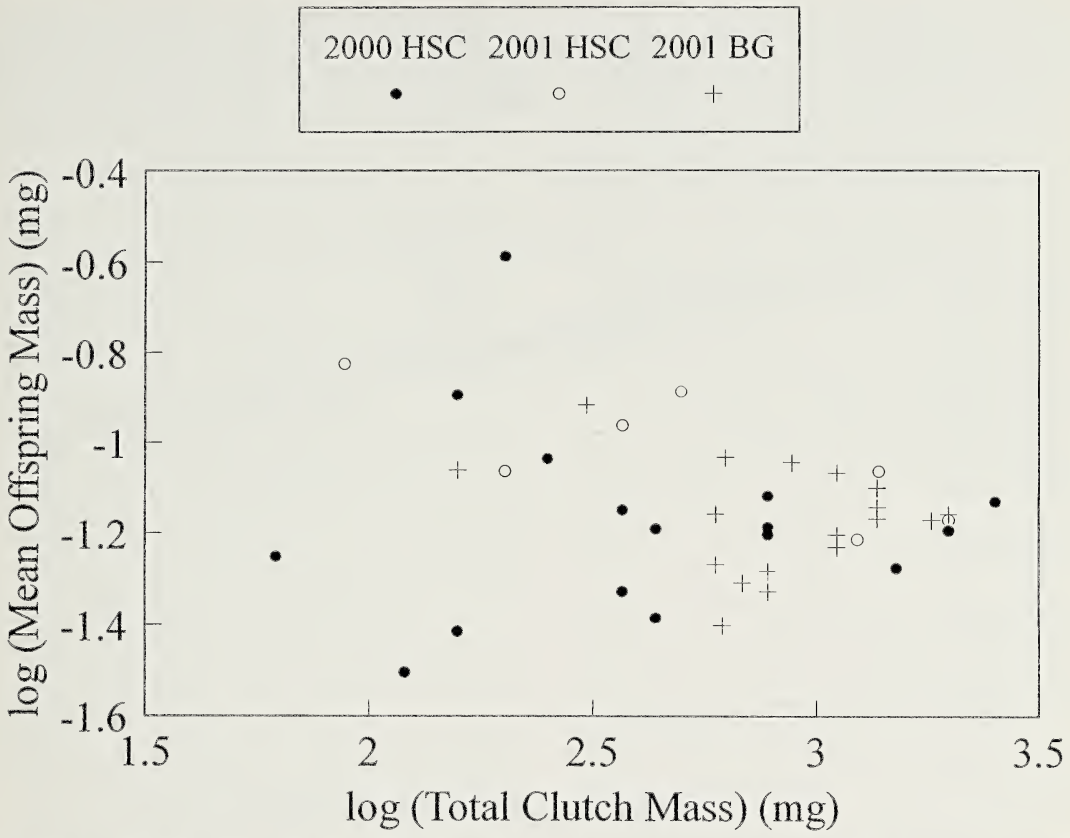


Figure 6.—Correlations between total clutch mass and mean offspring mass (both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Correlations: 2000 Hardscrabble Creek: $r = -0.20$, $P = 0.46$, $n = 16$; 2001 Hardscrabble Creek: $r = -0.76$, $P = 0.046$, $n = 7$; Ball Gulf: $r = -0.20$, $P = 0.42$, $n = 18$.

that offspring size varies less among females than other traits, our results indicate that offspring size in *P. sedentarius* is relatively canalized compared to offspring number. This may represent an anatomical constraint, perhaps in the structure of the ovaries or epigynum, which limits egg size but is itself unrelated to female size. Alternatively, females may exhibit little variation in per-offspring allocation strategies. For example, females may provision eggs with some minimum amount of yolk necessary for survival until offspring dispersal (see Marshall & Gittleman 1994), in which case females can maximize clutch size dependent on their available energy stores. This latter scenario potentially establishes a conflict of interest between the female and her offspring (sensu Parker & Mock 1987; Godfray & Parker 1991), as larger offspring size increases early-life fitness (starvation resistance) in at least one species of spider (Tanaka 1995).

As predicted by much life history theory (Roff 1992, 2002; Stearns 1992), offspring size and number appear to trade off in *P. sedentarius*. However, as has been found in other arachnids (e.g., Simpson 1993; Brown 2001), the strength of this trade-off within a species may vary among populations or over time. For example, our results at Hardscrabble Creek echo those of Simpson (1993) on the arctic lycosid *Pardosa glacialis* (Thorell 1872). He found that *P. glacialis* exhibited a trade-off in one year of his study but not another [and he found no trade-off in a second species, *Alopecosa hirtipes* (Kulczynski 1908), during either year]. There exist relatively few intraspecific studies of the size-number trade-off in spiders, with some documenting a size-number trade-off (e.g.,

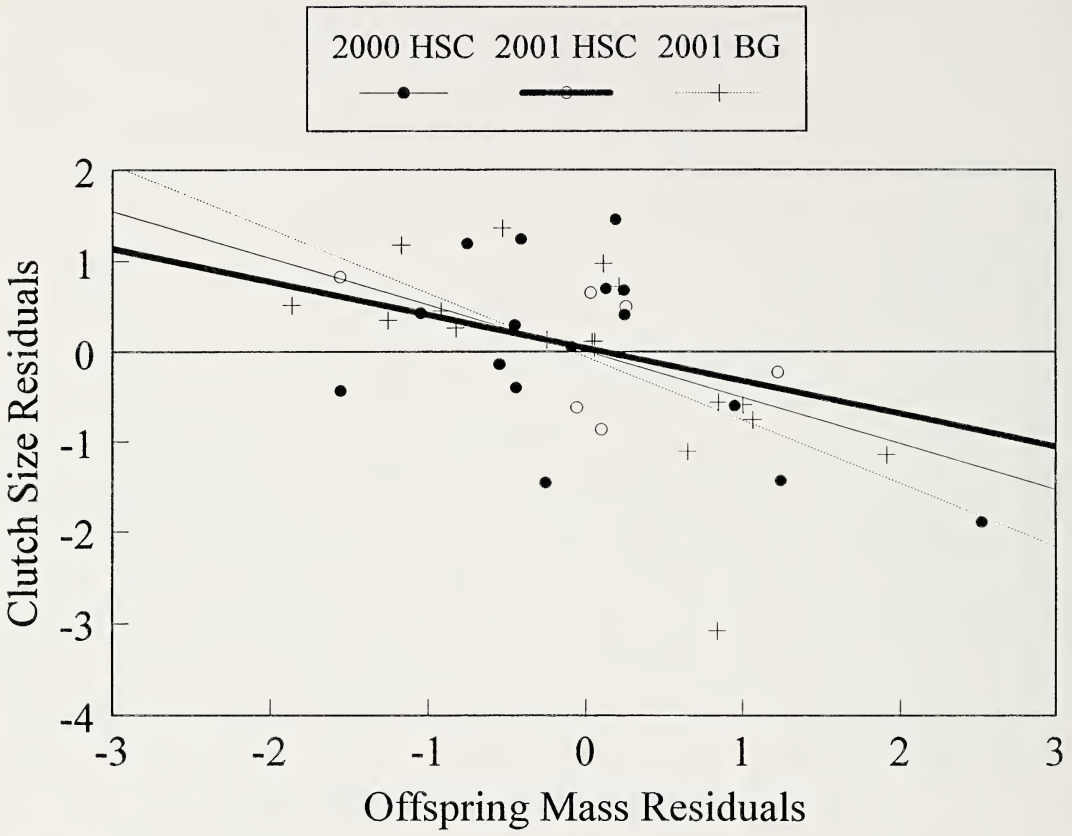


Figure 7.—Correlations between residual clutch size and residual offspring mass for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*.

Simpson 1993; Tanaka 1995) and others not (e.g., Fritz & Morse 1985; Simpson 1993).

The difficulty with consistently detecting a size-number trade-off in spiders may reflect the strong food limitation in many species (Wise 1993), such that many individuals will not obtain sufficient resources to produce a "normal" size or number of offspring. This may lead to a positive relationship between offspring size and number, if higher quality females (those obtaining the most resources) produce both more and larger offspring. It might also lead the trade-off slope to flatten out, if some (e.g., smaller) females are able to allocate a higher percentage of their resources to reproduction than other (e.g., larger) females because of differences in maintenance energy requirements. This situation could arise even if the latter (larger) females obtained equal or greater total amounts of resources. The relative canalization of offspring size might also help explain the lack of a size-number trade-off. If females all produce offspring of similar size, either because of an inability or unwillingness to deviate substantially from a species-specific egg size, then the underlying decision process for the trade-off (adding excess energy either to offspring already made or to the production of new offspring) is rendered moot. Instead, females will simply make as many offspring of a given, perhaps minimally viable, size as their resources allow. Regardless of mechanism, determining why, how, and under what circumstances trade-offs occur remains a critical challenge for the understanding of arachnid life history evolution.

ACKNOWLEDGMENTS

Pasha Apontes helped collect spiders during the summer of 2001. We thank the following for providing us with information on *Pirata* references: James Cokendolpher, Fred Coyle, Nancy Kreiter, Margaret Janowski-Bell, Don

Buckle, Theo Blick, Volker Framenau, and especially Peter Smithers and David Mayntz for the citations from BAZAR. We also thank two anonymous referees for their critical comments on the first draft.

LITERATURE CITED

Austin, A.D. 1984. Life history of *Clubiona robusta* L. Koch and related species (Araneae, Clubionidae) in South Australia. Journal of Arachnology 12:87–104.

Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. American Zoologist 36:216–236.

Briceño, R. 1987. How spiders determine clutch size. Revista de Biologia Tropical 35:25–29.

Brown, C.A. 2001. Allometry of offspring size and number in scorpions. Pp. 307–315. *In* Scorpions 2001. In Memoriam Gary A. Polis. (V. Fet & P. A. Selden, eds.). British Arachnological Society, Burnham Beeches, United Kingdom.

Buddle, C.M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. Journal of Arachnology 28:319–328.

Christians, J.K. 2000. Trade-offs between egg size and number in waterfowl: an interspecific test of the van Noordwijk and de Jong model. Functional Ecology 14:497–501.

Clutton-Brock, T.H. 1991. The Evolution of Parental Care. Princeton University Press, Princeton, New Jersey.

Dondale, C.D. & J.H. Redner. 1990. The Insects and Arachnids of Canada. Part 17. The Wolf Spiders, Nurseryweb Spiders, and Lynx Spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Canadian Department of Agriculture Publications, Ottawa.

Eberhard, W. 1979. Rates of egg production by tropical spiders in the field. Biotropica 11:292–300.

Edgar, W.D. 1971. Seasonal weight changes, age structure, natality and mortality in the wolf spider *Pardosa lugubris* Walck. in central Scotland. Oikos 22:84–92.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Annals of the Entomological Society of America 69:991–998.

Ferguson, G.W. & C.H. Bohlen. 1978. Demographic analysis: a tool for the study of natural selection of behavioral traits. Pp. 227–243. *In* Conference on Behavior and Neurology of lizards. (N. Greenberg & P. MacLean, eds.). DHEW Publication No.(ADM) 77–491, Washington, DC.

Ferguson, G.W., K.L. Brown & V.G. DeMarco. 1982. Selective basis for the evolution of variable egg and hatchling size in some iguanid lizards. Herpetologica 38:178–188.

Flint, P.L., J.B. Grand & J.S. Sedinger. 1996. Allocation of limited reserves to a clutch: a model explaining the lack of a relationship between clutch size and egg size. Auk 113:939–942.

Foelix, R.F. 1996. Biology of Spiders. Second Edition. Oxford University Press, Oxford.

Fritz, R.S. & D.H. Morse. 1985. Reproductive success and foraging of the crab spider *Misumena vatia*. Oecologia 65:194–200.

Godfray, H.C.J. & G.A. Parker. 1991. Clutch size, fecundity and parent-offspring conflict. Philosophical Transactions of the Royal Society of London B 332:67–79.

Harrington, C.L. 1978. Field studies on reproduction in the funnel-web spider *Agelenopsis potteri* (Araneae; Agelenidae). Oikos 31:368–375.

Jakob, E.M., S.D. Marshall & G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Kaston, B.J. 1946. Spiders of Connecticut. Connecticut State Geological and Natural History Survey, Bulletin No. 70.

Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia 8:93–109.

Killebrew, D.W. & N.B. Ford. 1985. Reproductive tactics and female body size in the green lynx spider, *Peucetia viridans* (Araneae, Oxyopidae). Journal of Arachnology 13:375–382.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8: 118–124.

McLay, C.L. & T.L. Hayward. 1987. Reproductive biology of the intertidal spider *Desis marina* (Araneae: Desidae) on a New Zealand rocky shore. Journal of Zoology 211:357–372.

Morse, D. 1988. Relationship between crab spider *Misumena vatia* nesting success and earlier patch-choice decisions. Ecology 69:1970–1973.

Nørgaard, E. 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. Oikos 3:1–21.

Nussbaum, R.A. 1981. Seasonal shifts in clutch-size and egg-size in the side-blotched lizard, *Uta stansburiana* Baird and Girard. Oecologia 49:8–13.

Parker, G.A. & D.W. Mock. 1987. Parent-offspring conflict over clutch size. Evolutionary Ecology 1:161–174.

Petersen, B. 1950. The relation between size of mother and number of eggs and young in some spiders and its significance for the evolution of size. Experientia 6:96–98.

Prenter, J., R.W. Elwood & W.I. Montgomery. 1999. Sexual size dimorphism and reproductive

investment by female spiders: a comparative analysis. Evolution 53:1987–1994.

Punzo, F. & L. Henderson. 1999. Aspects of the natural history and behavioral ecology of the tarantula spider, *Aphonopelma hentzi* (Orthognatha, Theraphosidae). Bulletin of the British Arachnological Society 11:121–128.

Roff, D.A. 1992. The Evolution of Life Histories. Chapman & Hall, New York.

Roff, D.A. 2002. Life History Evolution. Sinauer Associates, Sunderland, Massachusetts.

Simpson, M.R. 1993. Reproduction of two species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. Canadian Journal of Zoology 71: 451–457.

Simpson, M.R. 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology 76:795–800.

Smith, C.C. & S.D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

StatSoft. 1993. Statistica for Windows, version 4.5. StatSoft, Tulsa, Oklahoma.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Suter, R.B. 1990. Determinants of fecundity in *Frontinella pyramitela* (Araneae, Linyphiidae). Journal of Arachnology 18:263–269.

Tanaka, K. 1992. Life history of the funnel-web spider *Agelena limbata*: web site, growth, and reproduction. Acta Arachnologica 41:91–101.

Tanaka, K. 1995. Variation in offspring size within a population of the web-building spider *Agelena limbata*. Researches in Population Ecology 37: 197–202.

van Noordwijk, A.J. & G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

Vollrath, F. 1987. Growth, foraging, and reproductive success. Pp. 357–370. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Wallace, H.K. & H. Exline. 1978. Spiders of the genus *Pirata* in North America, Central America and the West Indies (Araneae, Lycosidae). Journal of Arachnology 5:1–112.

Whitcomb, W. 1967. Wolf and lynx spider life histories. Terminal report to the National Science Foundation, Washington, DC.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge, UK.

Yu, P., J. Zhao & H. Cui. 2001. The morphological characters and growth of spiderlings of *Pirata piraticus* (Clerck). Acta Arachnologica Sinica 10:22–25.

Manuscript received 1 July 2001, revised 11 December 2002.

2003. The Journal of Arachnology 31:297–304

NATURAL HISTORY OF *MISUMENOPS ARGENTEUS* (THOMISIDAE): SEASONALITY AND DIET ON *TRICHOGONIOPSIS ADENANTHA* (ASTERACEAE)

Gustavo Quevedo Romero and **João Vasconcellos-Neto**: Departamento de Zoologia, Universidade Estadual de Campinas (UNICAMP), C.P. 6109, Campinas, SP, 13083-970, Brazil, E-mail: gqromero@unicamp.br

ABSTRACT. Seasonal fluctuations, phenology and diet of *Misumenops argenteus* (Araneae, Thomisidae) on *Trichogoniopsis adenantha* (Asteraceae) were investigated in the Serra do Japi, southeastern Brazil, over a 2 year period. This spider population increased at the beginning of the rainy season, reaching a peak in March, and decreased in May, reaching its lowest density in the cold/dry season. In the rainy season (December–May), most of the individuals were in the young or juvenile phase (3rd–6th instars). The spiders reached adulthood between the end of the cold/dry season and the beginning of the hot/rainy season. Analysis of temporal displacement (with up to a 3 month delay) detected a one month delay between the blooming period of *T. adenantha* and the beginning of the rainy season. The number of arthropods (potential prey of *M. argenteus*) on the plants increased concomitantly with the increase in the number of reproductive branches. The *M. argenteus* population also increased numerically 2 months after the rise in arthropod density. These results indicate that the spiders require time to respond to changes in environmental conditions. Of the 595 spiders examined, 76 (12.8%) had prey. Prey items included arthropods belonging to several guilds, but spiders showed a preference for wingless prey or prey that remained on the branches for longer periods of time.

Keywords: Prey, seasonal distribution, plant-animal interactions

A single plant species can serve as a food resource for several different organisms. However, this resource can vary seasonally in abundance and quality (Begon et al. 1996; Espírito-Santo & Fernandes 1998). Frequently, plant-consuming insects are synchronized with the abundance of food, as well as with environmental conditions such as temperature and humidity (Wolda 1988; Vasconcellos-Neto 1991; Bernays & Chapman 1994). Predators, such as spiders, can adjust their phenology in response to abiotic conditions (Crane 1949; Plagens 1983; Rinaldi & Forti 1997; Rossa-Feres et al. 2000; Arango et al. 2000) and the availability of prey (Riechert & Luczak 1982; Plagens 1983; Riechert & Harp 1987; Costello & Daane 1995; Arango et al. 2000) and foraging sites (Plagens 1983; Arango et al. 2000). The thomisid crab spiders are sit-and-wait predators that frequently forage on flowers and leaves (see Foelix 1996). These spiders tend to choose their foraging sites based on the availability of food items (Morse & Fritz 1982; Morse 1984) since, when in optimal sites, they prey indiscriminately on several groups of arthropods (Dean et al. 1987; Agnew & Smith 1989; Lockley et al. 1989; Nyffeler & Breene 1990).

Misumenops argenteus (Rinaldi) (Thomisidae) occurs on several plant species, but uses the reproductive branches of *Trichogoniopsis adenantha* (DC.) as foraging sites more frequently (Romero 2001). In this study, we examined the seasonal fluctuations and phenology of *M. argenteus* on *T. adenantha*, and assessed whether these phenomena were synchronized with the seasonality of biotic and abiotic factors such as the period of plant blooming (which corresponds to the availability of foraging sites), the availability of arthropods (potential prey) associated with this plant and rainfall. We also investigated whether *M. argenteus* captured its prey non-selectively relative to the potential prey available.

METHODS

Study site and organisms.—This work was done along the edges of the Mirante track (elevation 1170 m), in the Serra do Japi (23°11′S, 46°52′W), close to the city of Jun-

diaí, in southeastern Brazil. The climate is seasonal, with a mean monthly temperature varying from 13.5 °C in July to 20.3 °C in January. The driest months are from June–September (Pinto 1992). The local vegetation is characterized by high elevation semi-deciduous mesophile forest, with canopy height varying between 10–15 m, and very dense undergrowth containing specific plant species (Leitão-Filho 1992).

Trichogoniopsis adenantha is a perennial shrub species (0.2–1.8 m high) that occurs along the forest margins in the Serra do Japi. This species produces up to seven pink or lilac-colored flowerheads (yellowish in the predispersal phase) arranged in racemes, but with desynchronized development, such that given branch often has flowerheads in different phenophases. These flowerheads attract arthropods belonging to several guilds including pollinators, herbivores, parasitoids and predators (Romero 2001). *Trichogoniopsis adenantha* blooms throughout the year with peak flower production occurring in the hot/rainy season (Almeida 1997). Consequently, the availability of food resources and foraging sites for *M. argenteus* can vary seasonally. *Misumenops argenteus*, a small, yellowish crab spider, is the principal predator on *T. adenantha*, where it becomes cryptic. Romero (2001) showed that the frequency of this spider on reproductive branches of this plant is 2.6-fold higher than on vegetative ones.

Voucher specimens of the spiders collected (males and females) were deposited in the Arachnological Collection of the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo.

Population fluctuation and phenology of *M. argenteus*.—The seasonal fluctuation of *M. argenteus* was determined as the variation in spider density (number of individuals/500 branches) throughout the year. The population phenology was determined based on temporal variations in age structure over the same time period (e.g. Peck 1999). To determine age structure, each *M. argenteus* found was classified as 1) young [total body length (cephalothorax + abdomen) $\leq$ 3.0 mm; 3rd and 4th instars], 2) juvenile ($>$ 3.0 mm but $\leq$ 4.5 mm; 5th and 6th instars), 3) subadult ($>$ 4.5 mm but $\leq$ 5.0 mm, or when the male had a dilated palp; 7th instar), or 4) adult ($>$ 5.0 mm, and/or when there were sclerotized genitalia; 8th instar). These data were used to construct a phenogram of the maturation and recruitment of individuals during the life cycle of this species. To study the populational parameters of *M. argenteus*, between 17 and 26 individuals of *T. adenantha* (height from 0.2 m–1.8 m) per study day were sampled during biweekly visits along a 1 km transect of the Mirante track. The first plant found at the end of each 20 m interval was inspected to ensure random sampling. Each plant was inspected for 3–10 min, depending on its size. The population of *T. adenantha* along this 1 km transect consisted of at least 400 individuals.

Synchrony and displacement between events.—To study the synchrony between the phenologies of *M. argenteus* and *T. adenantha*, the number of vegetative branches ($\geq$ 5 cm long) and reproductive branches of all the plants inspected was scored. The branches were classified as reproductive when they had at least one flowerhead. Branches with flowerheads only in the seed-dispersal phase were excluded from the analysis because they do not attract floral visitors or *M. argenteus* (Romero 2001).

Prey.—The availability of potential prey for *M. argenteus* was assessed by recording of all arthropods occurring on *T. adenantha* during a one hour period, usually between 10:30 h and 13:30 h, in biweekly inspections from December 1998–March 2000. Arthropods were identified to the genus, family or superfamily level. Arthropods not identified in the field and the food items of *M. argenteus* were fixed in 70% ethanol and identified in the laboratory. Rainfall data were obtained from the experimental station at Jundiaí, located 8 km from the study area.

Statistical analysis.—Relationships between the density of *M. argenteus* and rainfall, phenology of *T. adenantha* (number of reproductive branches/plant) and prey density (number/hour) were examined using the Pearson correlation test (Zar 1996) with $\alpha = 0.05$. The same comparisons were done separately for the density of young, juvenile, subadult and adult spiders. The data, expressed as proportions, were normalized by log or log (n + 1) transformation. Since organisms generally need time to respond to environmental changes (e.g. Arango et al. 2000), the correlation between different variables and time was also examined. To verify whether *M. argenteus*

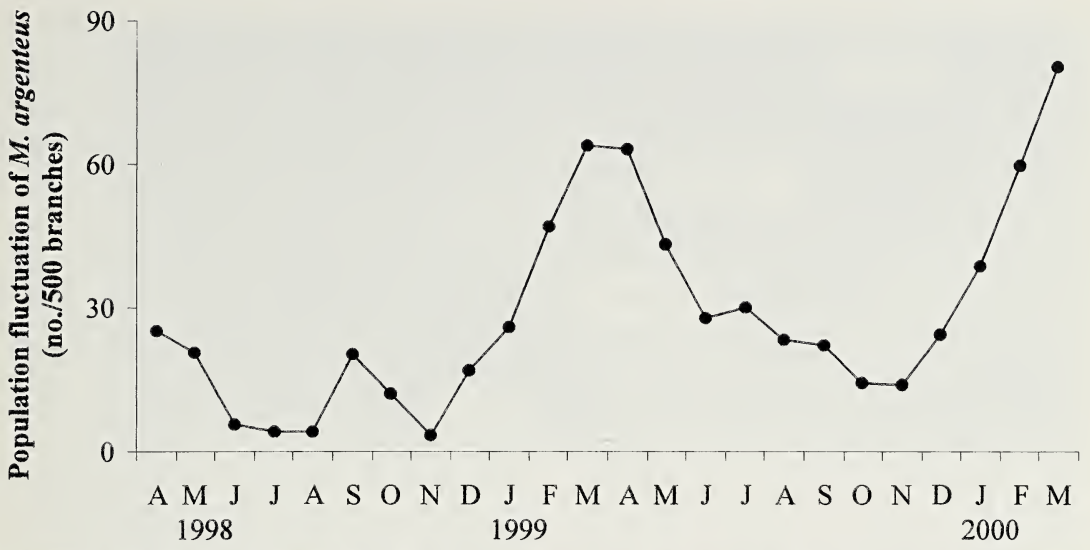


Figure 1.—Population fluctuation of *Misumenops argenteus* (Thomisidae) on *Trichogoniopsis adenantha*, from April 1998–March 2000, along the Mirante track, Serra do Japi. (n = 595 individuals).

chose prey at random, the range of prey used was compared with the distribution of available arthropods determined by the field observations using a G-test (Zar 1996). The preference and rejection of each prey item by *M. argenteus* was evaluated using Manly's α index of dietary preference for a constant prey population (Krebs 1999) based on the formula

$$\alpha_i = \frac{r_i}{n_i}\left[\frac{1}{\sum (r_i/n_i)}\right]$$

where α_i = Manly's index for prey type i, r_i and r_j = proportion of prey type i or j in the diet, and n_i and n_j = proportion of prey type i or j in the environment. A preference, detected as a deviation from the random sample of the prey, was indicated by values of $\alpha_i > 1/m$ (m = total number of prey types). In contrast, avoidance was indicated by values of $\alpha_i < 1/m$. This index is appropriate when the number of prey captured is much smaller than the total number of prey available (see Krebs 1999).

RESULTS

Population fluctuation and phenology of *M. argenteus*.—The population size of *Misumenops argenteus* started to increase at the beginning of the hot/rainy season (November) and reached a peak in March. The number of individuals decreased in May to reach the lowest density in the cold/dry season (July–September) (Fig. 1). In the rainy season, most individuals were in the young and juvenile phases (3rd–6th instars). Adulthood was reached between the end of the cold/dry season (June–July) and the beginning of the hot/rainy season (December–January) (Fig. 2).

Population recruitment occurred in November and December (Fig. 2). Young were present from October–April, with a peak in December–January. The proportion of juveniles started to increase in February and decreased between July and September. Subadults occurred in highest proportions in August and declined from November–December. The adult population was largest from July to November–December, with a peak in September 1998 and in October–November 1999 (Fig. 2). Young and juveniles together represented 70%–80% of the total number of *M. argenteus*, while subadults and adults were most frequent in the periods with a reduced population size (Figs. 1, 2).

Synchrony and displacement between events.—After the cold/dry season, the first rains occurred in September, but intensified from December–March (Fig. 3). The greatest abundance of reproductive branches in *T. adenantha* occurred from November–March, while that of arthropods occurred from March–May and in November and December; the number of *M. argenteus* peaked in March and April (Figs. 1, 3).

The numbers of flowering branches and rainfall were correlated in the same month ($r = 0.51$; $n = 16$; $P = 0.043$), or with the subsequent month, i.e., a temporal displacement of one month ($r = 0.85$; $n = 15$; $P < 0.001$). There was no correlation between arthropod density and rainfall in the same month, or after one, two or three months ($P = 0.66$; $P = 0.90$; $P = 0.54$ and $P = 0.44$, respectively), but there was a slight trend only between arthropod density and the density of reproductive branches in the same month ($r = 0.43$; $n = 16$; $P = 0.09$). The density of *Misumenops argenteus* correlated with rainfall only after three months ($r = 0.75$; $n = 13$; $P = 0.003$), with reproductive branches only after two months ($r = 0.79$; $n = 14$; $P < 0.001$), and with arthropod density only after two months ($r = 0.57$; $n = 14$; $P = 0.035$).

The density of young *M. argenteus* was positively correlated with rainfall in the same month ($r = 0.53$; $n = 24$; $P = 0.007$), and with arthropod density after three months ($r = 0.55$; $n = 13$; $P = 0,05$), but not with the number of reproductive branches for a time displacement of less than three months ($P \geq 0.08$). The density of juveniles was correlated with rainfall after two months ($r = 0.66$; $n = 22$; $P = 0.001$), but not with the number of reproductive branches, nor with arthropod density for a time displacement of less than three months ($P > 0.1$). The density of subadults and adults was not correlated with rainfall, with the number of reproductive branches, or with arthropod density for a time displacement of less than three months ($P > 0.1$).

Prey.—Of the 595 *M. argenteus* examined, 76 (12.8%) were feeding (Table 1). The prey consisted of herbivores (43.5%), pollinators (8%), parasitoids (12%), and predators (23%); 10.5% were eventuals (arthropods that occurred randomly on *T. adenantha*).

Misumenops argenteus fed mostly (84%) on the families (or genera) of arthropods that typically occurred on *T. adenantha* (Table 1). However, the use of arthropod prey was not random (Table 1; $G = 48.42$; 16 df; $P < 0.0001$) since there was a tendency to use more Grillidae sp., Ctenuchinae, Braconidae, ants and Chironomidae than predicted by Manly's index (Table 1). In contrast, *M. argenteus* used fewer Miridae sp. 1, Hoppers, Ithomiinae, Reduviidae sp. and Muscoidea than predicted by Manly's index (Table 1). There was no predation on *Melanagromyza* sp., Miridae sp. 2, Syrphidae spp. and Apoidea spp. (Table 1). Most of the ants and chironomid flies observed ($\approx$ 90%) were glued in the glandular trichomes of *T. adenantha*.

DISCUSSION

Population fluctuation, phenology, synchrony and displacements.—There was a one month delay between the beginning of the rains and the increase in the number of reproductive branches in *T. adenantha*, as well as in the synchrony between the number of reproductive branches and the increase in arthropod density. In contrast, a displacement of two months occurred between the increase in arthropod density (potential prey for *M. argenteus*) and the increase in spider population size. Similar results were obtained by Arango et al. (2000) in a system involving *Cnidoscolus aconitifolius* (Mill.) I.M. Johnstone (Euphorbiaceae), floral visitors and *Peucetia viridans* Hentz (Araneae, Oxyopidae). Climatic changes were probably the primary factor molding *T. adenantha* phenology, as also observed for several other plant species in the study area (Morellato et al. 1990; Morellato & Leitão-Filho 1990, 1992). The reproductive branches and flowerheads used as foraging sites by *M. argenteus* (Romero 2001) supplied food for several herbivore and pollinator species. If this resource become scarce during some period of the year, the insects directly dependent on it also become scarce. Consequently, the carrying capacity of the habitat (*T. adenantha*) for *M. argenteus*, expressed as the availability of foraging sites and prey, diminishes, thereby reducing the spider population size.

The density of young increased in the same month as rainfall. It is probable that eggsacs, although not frequently observed, were deposited in September and October, the beginning of the rainy season. These results suggest that rainfall is a stimulus for mating and egg laying, as seen with other errant spiders (Crane 1949; Rossa-Feres et al. 2000).

Prey.—Thirteen percent of the *M. argenteus* found were feeding. The population studied showed the same rate of prey capture when compared with reports for other Thomisidae (Dean et al. 1987; Nyffeler & Breene 1990). *Misumenops argenteus* fed on a wide

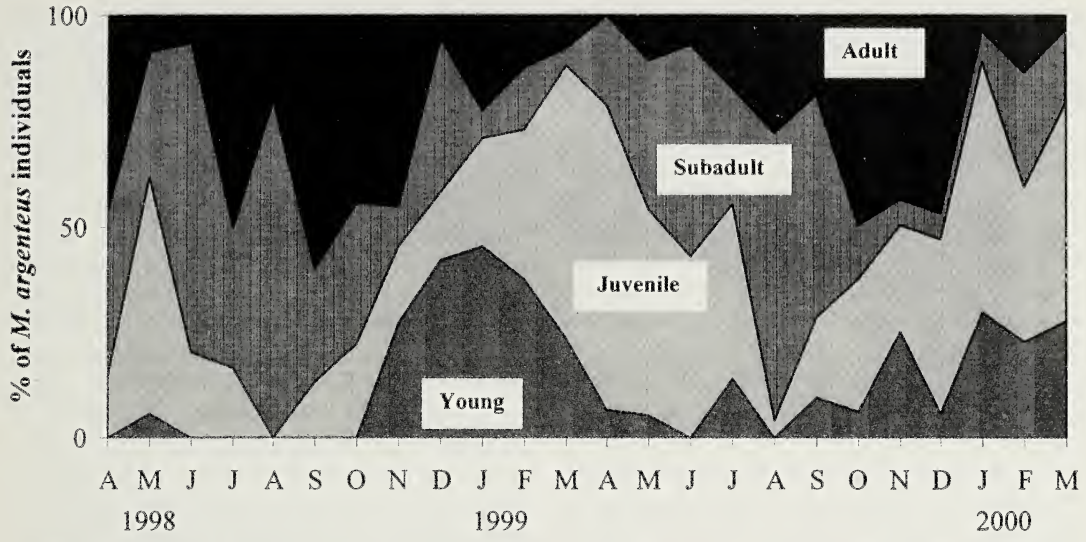


Figure 2.—Phenogram of the age structure of *Misumenops argenteus* (Thomisidae) population on *Trichogoniopsis adenantha* (Asteraceae), from April 1998–March 2000, along the Mirante track, Serra do Japi. (n = 595 individuals).

range of food items. Similar results have been described for other Thomisidae, including *Xysticus cristatus* (Clerck), *X. kochi* Thorell, *Misumenops celer* (Hentz) and *Misumena vatia* (Clerck) (Dean et al. 1987; Agnew & Smith 1989; Lockley et al. 1989; Nyffeler & Breene 1990). This polyphagy in *M. argenteus* may reflect the large variety of available prey, as described by Tanaka (1991) for *Agelena limbata* Thorell.

Despite the wide range of prey types captured, *M. argenteus* did not select prey randomly. In general, spiders avoid ants because of the potential damage that this prey can

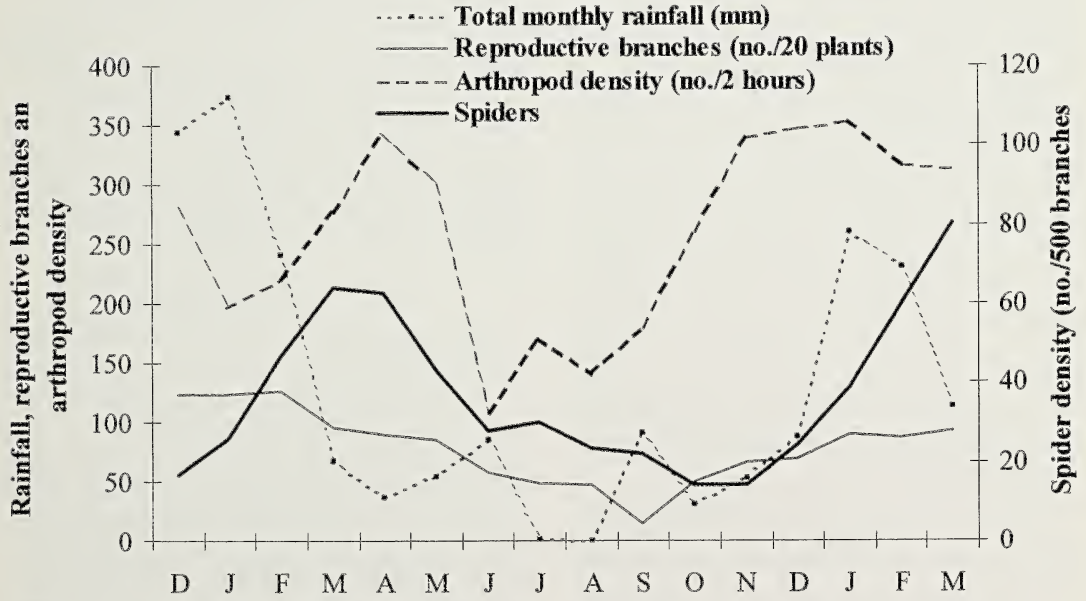


Figure 3.—Rainfall, number of reproductive branches (with flowerheads) per 20 *Trichogoniopsis adenantha* plants, arthropod density on the plants and *Misumenops argenteus* density (no./500 reproductive and vegetative branches), from December 1999–March 2000, along the Mirante track, Serra do Japi.

cause the predator (Riechert & Luczak 1982). However, *M. argenteus* captured more ants than the value expected (17% of all prey). Although ants occur only randomly on *T. adenantha*, the probability of spiders encountering ants is high because ants remain for longer periods and move around more on the plants than winged insects. Moreover, the glandular trichomes, which are very dense in *T. adenantha*, can reduce the velocity of the ants by sticking to these insects, making them easy for the spider to capture. Approximately 90% of the ants observed on the plants were stuck in the glandular trichomes and *M. argenteus* was seen preying on them ($n = 2$). In addition, almost all of the Chironomidae, also frequently used by *M. argenteus*, were stuck in the glandular trichomes. Like ants, Grillidae sp. and Braconidae also remain for longer periods on the plants. The Grillidae sp. lives amongst the leaves and flowerheads of *T. adenantha* and rarely flies, and the Braconidae spend a long time to laying eggs in endophagous insects in the flowerheads (G.Q. Romero, pers. obs.). Thus, insects that spent longer periods on the plants were more easily captured by the spiders.

In contrast, *M. argenteus* captured very few Miridae sp.1, hoppers and Reduviidae sp. relative to the expected value, and did not capture *Melanagromyza* sp., a small, very agile fly that can easily escape from the spiders (Romero 2001). Most of the hoppers on *T. adenantha* ($\approx$ 60–70%) belonged to the family Membracidae, which is frequently tended by large ants of the genus *Camponotus*. These ants, which are not captured by the crab spider and are not affected by the glandular trichomes (G.Q. Romero, pers. obs.), may protect the membracid hoppers against the spiders. The Reduviidae sp. was probably not captured by the crab spider because the latter forages primarily on reproductive branches whereas the former forages primarily on vegetative branches. In addition, the Reduviidae sp. population peaked in the cold/dry season (Romero 2001).

Misumenops argenteus captured more Ctenuchinae (Arctiidae) and fewer Ithomiinae, both of which are lepidopteran floral visitors, even though the latter group was more abundant than the first. Insects of both groups are similar in size, and both sequester pyrrolizidine alkaloids from the host plant to use in their defense against predation by spiders (Trigo 2000). The legs of ithomiines are very long, compared to the ctenuchine, and this may help them escape the spiders when they land on the flowerheads. Whereas some errant spider species (*Lycosa ceratiola* Gertsch & Wallace and tarantulas) or orb-spiders (*Nephila clavipes* (Linnaeus)) avoid pyrrolizidine alkaloids (reviewed in Trigo 2000), *M. argenteus* captures and consumes ctenuchines that contain such alkaloids in their exoskeleton (J.R. Trigo, pers. comm.). In contrast to spiders which masticate their prey (including exoskeleton), thomisid spiders, such as *M. argenteus*, suck their prey dry, leaving the exoskeleton intact (Pollard 1993). This could explain why *M. argenteus* does not avoid prey with defensive chemicals confined to the exoskeleton compared to spiders which masticate their prey and avoid such insects.

In conclusion, rainfall was the principal abiotic factor that influenced the trophic interactions in the *T. adenantha*—arthropod–spider system. With increased rainfall, the plants increased their production of reproductive branches that subsequently attracted and supported populations of plant-dwelling arthropods which in turn supported the *M. argenteus* population. These results indicate that a strong bottom-up effect influences the system. However, experiments by Romero (2001) showed *M. argenteus* to be effective in diminishing herbivore density and in enhancing the fitness of *T. adenantha*, thus indicating that top-down effects also act to structure this system. These results show the importance of interactions between biotic and abiotic factors in determining the structure of arthropod community associated with *T. adenantha*.

ACKNOWLEDGMENTS

The authors thank T.M. Lewinsohn, J.E.C. Figueira, M.A. Garcia, D. de C. Rossa-Feres, A.V. Freitas, E. Ramires, V. Schmalhofer and an anonymous reviewer for their advice and criticisms on the manuscript. A.A. Lise kindly identified the crab spider. G. Q. Romero was supported by a grant from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, grant no. 98/15854-3). J. Vasconcellos-Neto was supported by a grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant no. 300539/94-0).

Table 1.—Prey available to and captured by *Misumenops argenteus* on *Trichogoniopsis adenantha* (Asteraceae), and the Manly's indices of dietary preference. Indices greater or smaller than 0.059 (1/total number of prey types) indicate preference or avoidance by the spider, respectively (see Methods). [a] = Insects consumed but not sampled in the biweekly observations. "Eventuals" = arthropods that occurred randomly on the plants.

	Prey				Manly's index
	Available	(%)	Captured	(%)	
Herbivores					
Endophages					
Melanagromyza sp. (Dip.)	136	8.5	0	0	—
Xantaciura sp. (Dip.)	26	1.6	2	2.6	0.053
Trupanea sp. (Dip.)	29	1.8	1	1.3	0.024
Cecidomyiidae spp. (Dip.)[a]	0	0	3	3.9	—
Suckers					
Miridae sp.1 (Het.)	345	21.6	7	9.2	0.014
Miridae sp.2 (Het.)	29	1.8	0	0	—
Aphididae spp. (Hom.)	86	5.4	6	7.9	0.048
Hoppers (Hom.)	73	4.6	2	2.6	0.019
Chewers					
Geometridae spp. (larvae) (Lep.)	131	8.2	7	9.2	0.037
Grillidae sp. (Ort.)	30	1.9	3	3.9	0.069
Chrysomelidae spp. (Col.)	47	2.9	2	2.6	0.029
Pollinators					
Ithomiinae spp. (Lep.)	79	4.9	2	2.6	0.017
Syrphidae spp. (Dip.)	13	0.8	0	0	—
Apoidea spp. (Hym.)	15	0.9	0	0	—
Ctenuchinae spp. (Lep.)	10	0.6	4	5.3	0.276
Parasitoids					
Braconidae spp. (Hym.)	52	3.2	5	6.6	0.066
Pteromalidae spp. (Hym.)	61	3.8	4	5.3	0.045
Predators					
Reduviidae sp.1 (Het.)	167	10.4	2	2.6	0.008
Araneae spp. (Arach.)	73	4.6	5	6.6	0.047
Formicidae spp. (Hym.)	87	5.4	13	17	0.103
Eventuals					
Chironomidae spp. (Dip.)	16	1.0	3	3.9	0.129
Muscoidea spp. (Dip.)	95	5.9	2	2.6	0.014
Coreidae sp. (Het.)[a]	0	0	1	1.3	—
Staphylinidae sp. (Col.)[a]	0	0	1	1.3	—
Carabidae sp. (Col.)[a]	0	0	1	1.3	—
Total	1600		76		

LITERATURE CITED

Agnew, C.W. & J.W. Smith. 1989. Ecology of spiders (Araneae) in a peanut agroecosystem. Environmental Entomology 18:30–42.

Almeida, A.M. 1997. Padrões de ocorrência em insetos endófagos associados a capítulos de *Trichogoniopsis adenantha* (DC) (Asteraceae). Masters Thesis, Universidade Estadual de Campinas, Campinas.

Arango, A.M., V. Rico-Gray & V. Parra-Tabla. 2000. Population structure, seasonality, and habitat use by the green lynx spider *Peucetia viridans* (Oxiopidae) inhabiting *Cnidoscolus aconitifolius* (Euphorbiaceae). Journal of Arachnology 28:185–194.

Begon, M., J.L. Harper & C.R. Townsend. 1996. Ecology. 3rd Ed. Blackwell Science, Oxford.

Bernays, E.A. & R.F. Chapman. 1994. Host-plant Selection by Phytophagous Insects. Chapman & Hall, New York.

Costello, M.J. & K.M. Daane. 1995. Spider (Araneae) species composition and seasonal abundance in San Valley Grape Vineyards. Environmental Entomology 24:823–831.

Crane, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. Zoologica 34:159–215.

Dean, D.A., W.L. Sterling, M. Nyffeler & R.G. Breene. 1987. Foraging by selected spider predators on the cotton fleahopper and other prey. Southwestern Entomology 12:263–270.

Espírito-Santo, M.M. & G.W. Fernandes. 1998. Abundance of *Neopelma baccharidis* (Homoptera: Psyllidae) galls on the dioecious shrub *Baccharis dracunculifolia* (Asteraceae). Environmental Entomology 27:870–876.

Foelix, R.F. 1996. Biology of Spiders. Second Edition, Oxford University Press, Oxford.

Krebs, C.J. 1999. Ecological Methodology. Second Edition, Addison Wesley Longman, Inc., California.

Leitão-Filho, H.F. 1992. A flora arbórea da Serra do Japi. Pp. 40–62. *In* História natural da Serra do Japi: ecologia e preservação de uma área florestal no Sudeste do Brasil (L.P.C. Morellato, ed.). Editora da Unicamp/Fapesp, Campinas.

Lockley, T.C., O.P. Young & J.L. Hayes. 1989. Nocturnal predation by *Misumena vatia* (Araneae, Thomisidae). Journal of Arachnology 17: 249–251.

Morellato, L.P.C. & H.F. Leitão-Filho. 1990. Estratégias fenológicas de espécies arbóreas de floresta mesófila na Serra do Japi, Jundiaí, São Paulo. Brazilian Journal of Biology 50:163–173.

Morellato, L.P.C. & H.F. Leitão-Filho. 1992. Padrões de frutificação e dispersão na Serra do Japi. Pp. 112—140. *In* História Natural da Serra do Japi: Ecologia e Preservação de uma Área Florestal no Sudeste do Brasil (L.P.C. Morellato, ed.). Editora da Unicamp/Fapesp, Campinas.

Morellato, L.P.C., H.F. Leitão-Filho, R.R. Rodrigues & C.A. Joly. 1990. Estratégias fenológicas de espécies arbóreas de floresta de altitude na Serra do Japi, Jundiaí, São Paulo. Brazilian Journal of Biology 50:149–162.

Morse, D.H. 1984. How crab spiders (Araneae, Thomisidae) hunt at flowers. Journal of Arachnology 12:307–316.

Morse, D.H. & R.S. Fritz. 1982. Experimental and observational studies of patch choice at different scales by the crab spider *Misumena vatia*. Ecology 63:172–182.

Nyffeler, M. & R.G. Breene. 1990. Spiders associated with selected European hay meadows, and the effects of habitat disturbance, with the predation ecology of the crab spiders, *Xysticus* spp. (Araneae, Thomisidae). Journal of Applied Entomology 110:149–159.

Peck, D.C. 1999. Seasonal fluctuations and phenology of *Prosapia* Spittlebugs (Homoptera: Cercopidae) in upland pastures of Costa Rica. Environmental Entomology 28:372–386.

Pinto, H.S. 1992. Clima na Serra do Japi. Pp. 30–38. *In* História Natural da Serra do Japi: Ecologia e Preservação de uma Área Florestal no Sudeste do Brasil (L.P.C. Morellato, ed.). Editora da Unicamp/Fapesp, Campinas.

Plagens, M.J. 1983. Populations of *Misumenops* (Araneae: Thomisidae) in two Arizona cotton field. Environmental Entomology 12:572–575.

Pollard, S. 1993. Little murders. Natural History 102:58–65.

Riechert, S.E. & J. Luczak. 1982. Spider foraging: behavioral responses to prey. Pp. 353–385. *In* Spider Communication: Mechanisms and Ecological Significance (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, New Jersey.

Riechert, S.E. & J.M. Harp. 1987. Nutritional ecology of spiders. Pp. 645–672. *In* Nutritional ecology of insects, mites, spiders, and related invertebrates (F. Slansky Jr. & J.G. Rodrigues, eds.). John Wiley & Sons, New York.

Rinaldi, I.M.P. & L.C. Forti. 1997. Hunting spiders of woodland fragments and agricultural habitats in the atlantic rain forest region of Brazil. Studies on Neotropical Fauna & Environment 32:1–12.

Romero, G.Q. 2001. Estudo experimental da associação de *Runcinioides argenteus* (Araneae, Thomisidae) em *Trichogoniopsis adenantha* (DC) (Asteraceae). Masters Thesis, Universidade Estadual de Campinas, Campinas.

Rossa-Feres, D. de C., G.Q. Romero, E. Gonçalves-de-Freitas & R.J.F. Feres. 2000. Reproductive behavior and seasonal occurrence of *Psecas viridipurpureus* (Salticidae, Araneae). Brazilian Journal of Biology 60:221–228.

Tanaka, K. 1991. Food consumption and diet composition of the web-building spider *Agelena limbata* in two habitats. Oecologia 86:8–15.

Trigo, J.R. 2000. Chemistry of defense against predation in neotropical Lepidoptera: facts, perspectives and caveats. Journal of Brazilian Chemical Society 11:551–561.

Vasconcellos-Neto, J. 1991. Interactions between Ithomiine butterflies and Solanaceae: feeding and reproductive strategies. Pp. 291–312. *In* Plant-animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions (P.W. Price, T.M. Lewinsohn, G.W. Fernandes & W.W. Benson, eds.).John Wiley & Sons, New York.

Wolda, K. 1988. Insect seasonality: why? Annual Review of Ecology and Systematics 19:1–18.

Zar, J.H. 1996. Biostatistical Analysis. 3rd Ed. Prentice Hall, Upper Saddle River, New Jersey.

Manuscript received 22 April 2002, revised 5 December 2002.

2003. The Journal of Arachnology 31:305–308

SHORT COMMUNICATION

EFFECTS OF MATERNAL BODY SIZE ON CLUTCH SIZE AND EGG WEIGHT IN A PHOLCID SPIDER (*HOLOCNEMUS PLUCHEI*)

Christa D. Skow: Neuroscience and Behavior Program, Tobin Hall, University of Massachusetts, Amherst, Massachusetts 01002 USA

Elizabeth M. Jakob: Department of Psychology, Tobin Hall, University of Massachusetts, Amherst, Massachusetts 01002 USA

ABSTRACT. The pholcid spider *Holocnemus pluchei* (Scopoli 1763) competes for food with conspecifics, and spiders reared on high food levels are generally larger. In this study, we examined whether larger female body size (as estimated by tibia-patella length) translated into increased reproductive success in the form of increased clutch size, clutch weight, and average egg weight. Larger spiders had more eggs and thus heavier clutches, but there was no relationship between maternal size and average egg weight. We also looked for a tradeoff between average egg weight and egg number, and we found a weak relationship in which average egg weight was highest for intermediate-sized clutches. Larger female body size thus translates into increased reproductive success in terms of egg number and clutch weight, but not weight of individual eggs.

Keywords: Pholcidae, fecundity, egg size, clutch size, fitness

Number and size of eggs produced are important components of spider fitness. Clutch size in most arthropod species, including spiders (Jann & Ward 1999; reviews in Marshall & Gittleman 1994; Simpson 1995) increases with female body size. In some arthropod species (Fox & Czesak 2000), including *Agelena limbata* Thorell (Tanaka 1995), females can alter investment in individual eggs based on maternal body size and condition, whereas in other arthropod species egg size is invariant (reviewed in Fox & Czesak 2000). Life history theory predicts tradeoffs between clutch size and offspring size (Smith & Fretwell 1974), although these are frequently not apparent (Fox & Czesak 2000).

We examined the effect of maternal body size on clutch size and average egg weight in the pholcid spider *Holocnemus pluchei*. (Scopoli 1763). The behavior and life history of this species is well known. Spiders often share webs and fight vigorously over prey and larger spiders generally win (Blanchong et al. 1995; Jakob 1991, 1994; Jakob et al. 2000). Spiders reared on higher prey levels grow to a larger size than spiders reared on lower prey levels, except for those on extremely limited food regimes that may add an additional instar before maturation (Jakob & Dingle 1990). Females in the laboratory readily mate multiply, and second male sperm priority predominates (Kaster & Jakob 1997). Because *H. pluchei* shifts webs frequently and it is difficult to follow marked individuals for extended periods, lifespan and total number of clutches in the field is unknown. In the laboratory, spiders often live for over a year, and we have occasionally observed individuals to lay multiple clutches (Jakob pers. obs.).

We were interested in linking more directly the behaviors of group living and fighting with their fitness consequences by establishing whether an increase in maternal body size translates into more eggs or heavier clutches. We were also interested in whether there were relationships among body size, clutch size and mean egg size. In other species, egg and offspring size has numerous fitness consequences, with larger generally being better (reviewed in Tanaka 1995). In *H. pluchei*, variation in offspring size or condition may have an additional consequence, because whether spiderlings join group webs or build their own webs depends significantly on their condition, which is in turn influenced by their recent feeding success (Jakob unpubl. data). Any variation in the resources allocated to individual eggs that affects the condition of the spiderlings might predispose newly independent individuals toward or away from group living.

During August of 1998, 57 female *Holocnemus pluchei* with egg sacs were collected on the campus

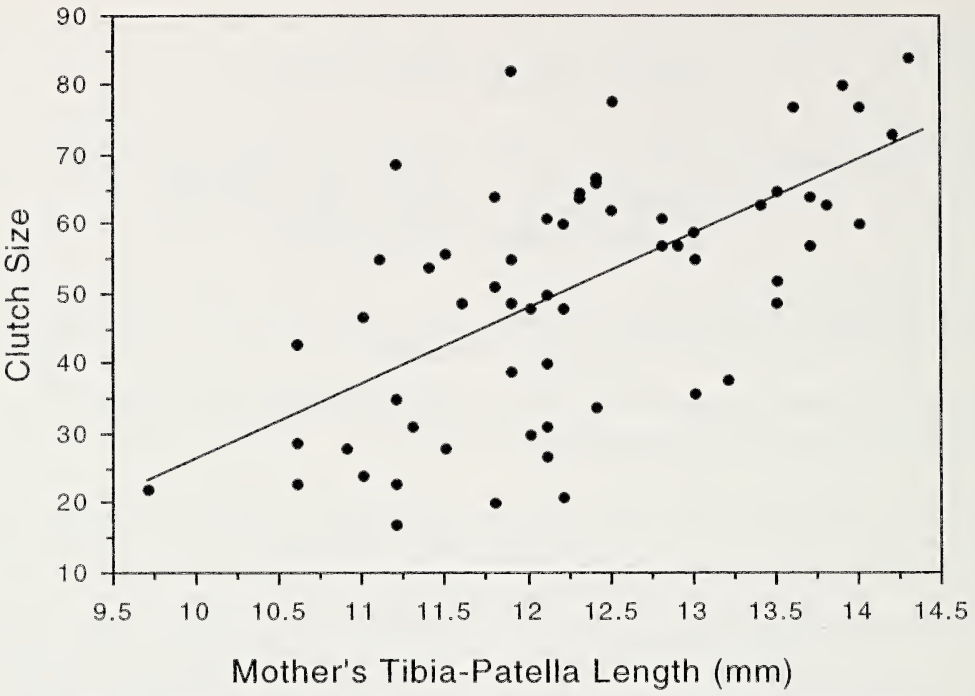


Figure 1.—Clutch size (number of eggs) regressed against mother's tibia-patella length.

of the University of California at Davis. Upon collection, 35 randomly chosen females were immediately anesthetized with carbon dioxide and preserved with their eggs in 95% ethanol in screw cap vials. The remaining 22 females were housed individually with their eggs as in Jakob (1991), and kept in growth chambers on a 15:9 L:D schedule with daytime temperatures of 32 °C and nighttime temperatures of 22 °C. All clutches hatched within four days of capture. Females normally do not feed while guarding and were not supplemented with food or water while in the chamber. When a clutch hatched, the female and her hatchlings were anesthetized with carbon dioxide and placed in screw cap vials (along with any unhatched eggs) with 95% ethanol for preservation. All samples were transported back to the University of Massachusetts at Amherst, where we measured female tibia-patella lengths of legs 1 and 2 with calipers, teased apart egg sacs and counted eggs, and counted hatchlings. After counting, we dried the females and their offspring in an oven at 128 °C for a minimum of 6 hours until they reached a constant weight. Samples were weighed on a microbalance within 24 hours of drying. Dried samples were kept in loosely capped vials in a sealed plastic container with silica gel (to prevent absorption of water) until being weighed. We weighed clutches rather than individual eggs or hatchlings because of the limits of scale accuracy. Some samples were inadvertently destroyed after counting and before weighing, so we weighed only 34 clutches of eggs and 22 clutches of hatchlings.

To estimate the size of the mother, we used female dry weight and tibia-patella lengths of legs 1 and 2. Tibia-patella length of leg 1 was highly correlated with leg 2 ($F_{1,60} = 892.76$, $R^2 = 0.968$, $P < 0.0001$), and with weight ($F_{1,60} = 80.391$, $R^2 = 0.573$, $P < 0.0001$), so for subsequent calculations we used only the tibia-patella length of leg 1.

We compared clutch size and clutch weight of offspring measured as eggs versus those measured as hatchlings and found no differences (clutch size: eggs 48 ± 2.8, hatchlings 53 ± 3.7, $F_{1,60} = 1.300$, $P > 0.2$; clutch weight: eggs 6.00 ± 0.002 mg, hatchlings 6.00 ± 0.002 mg, $F_{1,54} = 0.08$, $P > 0.7$). Nonetheless, because we were concerned that clutch weight might be affected by hatching, for all weight analyses we examined the two separate treatment groups as well as the pooled data. We found no qualitative differences in these analyses and present only the pooled data for brevity's sake.

We found that the mother's tibia-patella length of leg 1 significantly predicted both the number of eggs ($F_{1,60} = 36.574$, $R^2 = 0.379$, $P < 0.0001$, Fig. 1) and the total clutch weight ($F_{1,54} = 30.838$, $R^2 = 0.362$, $P < 0.0001$). The R^2 values indicate that a moderate amount of the variance is explained by maternal size, and is higher than or similar to that reported for other spiders (e.g., Buddle 2000; Tanaka 1995; Uetz and Hieber 1997).

These data provide a snapshot of a population in

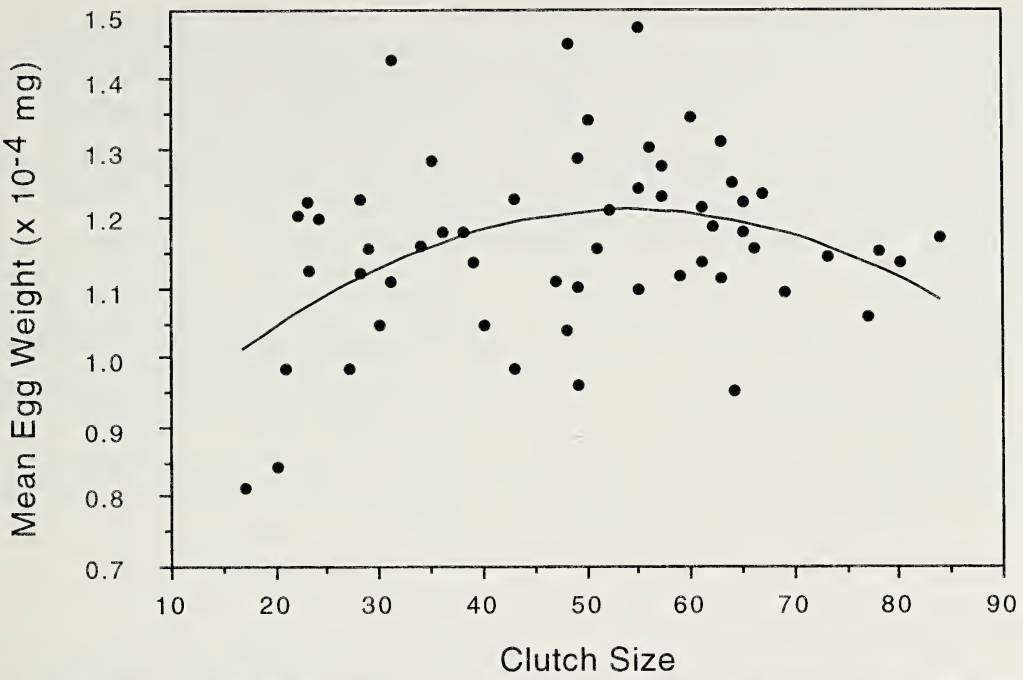


Figure 2.—Mean egg weight regressed against clutch size. There is no evidence of a classic egg weight/egg number tradeoff; average egg weight was highest for intermediate-sized clutches.

the field. Some of the variance probably results from the fact that our spiders were field caught. We could not control for many conditions likely to influence clutch size and weight, such as foraging history, temperature, female age and female parity (see Buddle 2000 for additional discussion). For example, spiders of all sizes are present year round, so it is likely that at the time of our collection in August there was a range of spider ages. In spite of this, the relationship between body size and clutch size is robust (Fig. 1), suggesting a fitness advantage of larger females under field conditions. However, if female size is negatively correlated with total number of clutches produced over a lifetime (e.g., if large females die younger) then this fitness benefit would be reduced or eliminated. This seems unlikely: in several cases where arthropod longevity and body size have been measured in the field, larger size correlates with longer lifespan, especially overwintering success (e.g., Ohgushi 1996).

We found no significant relationship between tibia-patella length and average egg weight ($F_{1,54}$ = 0.464, R^2 = 0.009, $P > 0.4$). In many arthropod populations, larger females lay larger eggs, but exceptions abound, and where there is a relationship it tends to be weak (reviewed in Fox & Czesak 2000). Given that our spiders were field caught and other important environmental variables were not controlled, we cannot definitively exclude a relationship between female body size and mean egg weight. However, we believe that a tradeoff is unlikely to be apparent under normal field conditions.

We looked for a tradeoff between egg size and number by regressing mean egg weight against clutch size. There was no significant linear relationship ($F_{1,55}$ = 2.905, $P > 0.09$). The data were best fit by a second order regression ($F_{3,55}$ = 3.455, R^2 = 0.166, $P < 0.01$, Fig. 2): intermediate clutch sizes had the highest mean egg weight. This is difficult to interpret, especially as different mechanisms may determine the shape of the curve at either end (for example, females in poor condition may only be able to lay few small eggs, whereas females laying large clutches may be constrained by abdominal volume). Only a small percent of the variance in mean egg weight is explained by clutch size. Other potential sources of variation include female age: in most arthropods, progeny size decreases with maternal age (Fox & Czesak 2000). Relationships between egg size and number can be difficult to detect because the total quantity of resources allocated to reproduction must be assumed to be constant, and this is unlikely to be true under field conditions (Fox & Czesak 2000). Further experiments will be needed to establish the robustness of this pattern and its underlying processes. In addition, the available microbalance did not allow us to measure individual eggs, and thus we cannot draw any conclusions about variation of egg size within female clutches.

In general, our findings are in line with the conclusions of Marshall & Gittleman (1994) that there is more flexibility in clutch size rather than egg size in spiders. Taken with previous studies of *H. pluchei* behavior and life history (Jakob & Dingle 1990), we conclude that there is a direct relationship between food intake, body size at maturity and reproductive success as measured by number of eggs and clutch weight. We have argued that spiders that are able to compete successfully for food have a selective advantage (Jakob 1991, 1994; Jakob et al. 2000), and this study provides additional support for this assumption for females.

ACKNOWLEDGMENTS

We thank B. Curtis for valuable assistance in the field. H. Dingle generously provided space in his laboratory. C. Yin kindly allowed us to use his balance, and D. Ferro loaned us his drying oven. We thank L. Baker, E. Wells, J. Houser, C. Hoefler, and A. Porter for comments on the manuscript, and M. Baker for insightful discussion. This study was supported by NSF IBN 95-07417 to EMJ.

LITERATURE CITED

Blanchong, J., M. Summerfield, M. Popson, & E. Jakob. 1995. Chivalry in pholcid spiders revisited. Journal of Arachnology 23:165–170.

Buddle, C. M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. Journal of Arachnology 28:319–328.

Fox, C. W. & M. E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45:341–369.

Jakob, E.M. 1991. Costs and benefits of group living for pholcid spiders: losing food, saving silk. Animal Behaviour 41:711–722.

Jakob, E. M. 1994. Contests over prey by group-living pholcids (*Holocnemus pluchei*). Journal of Arachnology 22:39–45.

Jakob, E., J. Blanchong, M. Popson, K. Sedey ,& M. Summerfield. 2000. Ontogenetic shifts in the cost of living in large groups: focal observations of a pholcid spider (*Holocnemus pluchei*). American Midland Naturalist 143:405–413.

Jakob, E.M. & H. Dingle. 1990. Food level and life history characteristics in a pholcid spider. Psyche 97:95–110.

Jann, P. & P.I. Ward. 1999. Maternal effects and their consequences for offspring fitness in the Yellow Dung Fly. Functional Ecology 13:51–58.

Kaster, J. and E.M. Jakob. 1997. Last-male sperm priority in a haplogyne spider: correlations between female morphology and patterns of sperm usage. Annals of the American Entomological Society 90:254–259.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8: 118–124.

Ohgushi, T. 1996. Consequences of adult size for survival and reproductive performance in a herbivorous ladybird beetle. Ecological Entomology 21:47–55.

Simpson, M.R. 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology 76:795–800.

Smith, C.C. & S.D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

Tanaka, K. 1995. Variation in offspring size within a population of the web-building spider *Agelena limbata*. Researches in Population Ecology 37: 197–202.

Uetz, G.W. & C.S. Hieber. 1997. Colonial web-building spiders: balancing the costs and benefits of group-living, Pp. 458–475. *In* The Evolution of Social Behavior in Insects and Arachnids. (J.C. Choe & B.J. Crespi,eds.) Cambridge University Press, Cambridge.

Manuscript received 12 September 2001, revised 11 December 2002.

2003. The Journal of Arachnology 31:309–315

SHORT COMMUNICATION

IS THE HAIRY GROOVE IN THE GIBBOSUS MALE MORPH OF *OEDOTHORAX GIBBOSUS* (BLACKWALL 1841) A NUPTIAL FEEDING DEVICE?

Danny Vanacker, Liesbeth Maes, Sylvia Pardo, Frederik Hendrickx: Laboratory of Animal Ecology, Zoogeography and Nature Conservation, Ghent University, Ledeganckstraat 35, 9000 Ghent, Belgium, E-mail: Danny.Vanacker@rug.ac.be

Jean-Pierre Maelfait: Laboratory of Animal Ecology, Zoogeography and Nature Conservation, Ledeganckstraat 35, 9000 Ghent, Belgium; Institute of Nature Conservation, Kliniekstraat 25, 1070 Brussels, Belgium

ABSTRACT. *Oedothorax gibbosus* (Blackwall 1841) (Erigoninae, Linyphiidae, Araneae) is a dwarf spider characterized by dimorphic males. There is a "gibbosus" male morph characterized by a hunch on the posterior third of the carapace, anterior to which is a hairy groove, and a "tuberosus" morph without these features. We observed several gustatorial courtship interactions by a gibbosus male morph and a conspecific female as well as a by a gibbosus male and a male of the closely related species, *Oedothorax fuscus* (Blackwall 1834). These interactions suggest that the hairy groove in the gibbosus male morph is a nuptial feeding device possibly under the influence of sexual selection. The interspecific interactions can possibly be interpreted as 'robbings' of the nuptial feeding. The interspecific interactions indicate that the cephalic structure of gibbosus probably does not function as a "lock and key" mechanism.

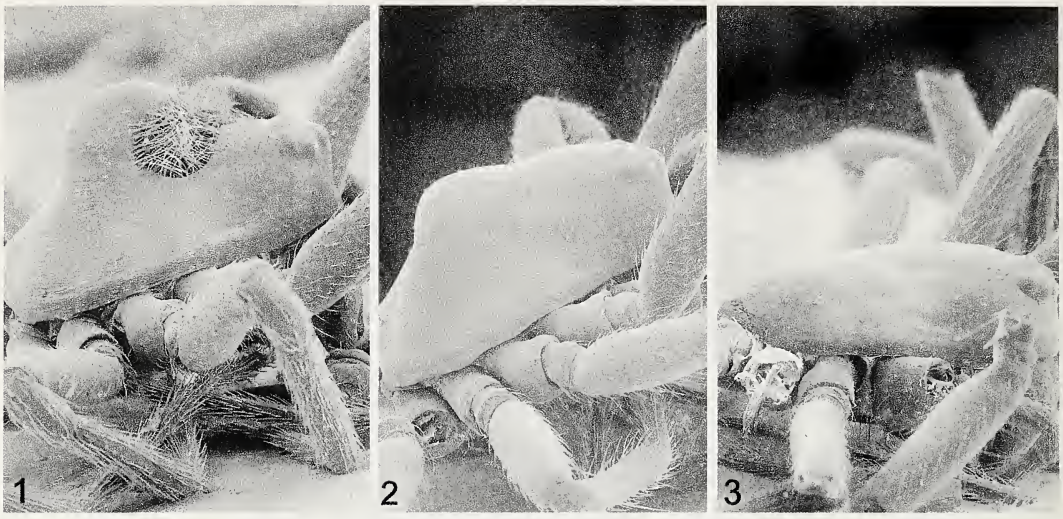
Keywords: *Oedothorax gibbosus*, *Oedothorax fuscus*, interspecific courtship, nuptial feeding, gustatorial courtship

Oedothorax gibbosus (Blackwall 1841) is a rare dwarf spider species in Flanders (northern part of Belgium) that occurs only in wet to very wet habitats (De Keer & Maelfait 1989; Maelfait et al.; 1998) such as oligo- and mesotrophic alder carrs. It lives between leaf litter and mosses in the immediate vicinity of open water. These habitats have become scarce in Belgium and therefore this species is known only from a few nature reserves, such as the public nature reserve "Het Walenbos" at Tielt-Winge (50° 55' NL, 4° 51' EL), 30 km northeast of Brussels, where our material was gathered.

Oedothorax gibbosus is a species with dimorphic males. In the gibbosus morph the carapace is raised in the foveal region to form a hunch. Between that protuberance and the eye region is a transverse groove surrounded and filled with long black and stiff hairs (Fig. 1). The tuberosus morph (Fig. 2) does not show any remarkable differentiation at the dorsal side of the carapace. Its carapace is only a bit more raised and convex than that of the female (Fig. 3), but lacks the deep notch and the long hairs. Voucher specimens of one *O. gibbosus* female, one gibbosus and tuberosus male morph and one male of *O. fuscus* are deposited in the collection the Royal Belgian Institute of Natural Sciences, Vautierstraat 29, Brussels, Belgium: IG29707.

Previously, the two morphs were considered to be different species, *Oedothorax gibbosus* (Blackwall 1841) and *Oedothorax tuberosus* (Blackwall 1841), that could only be distinguished on the basis of the morphology of the males. However, De Keer & Maelfait (1988) proved the male dimorphism in *Oedothorax gibbosus* when both morphs hatched from one cocoon collected in the field. The terminology of the old species names and the new male morph names refers to the dorsal cephalic differentiation of the male spiders.

Oedothorax gibbosus is not the only spider with a male dimorphism. According to Roberts (1987), in the subfamily Erigoninae there are three other dwarf spider species in Great Britain with a male dimorphism. In each of these species, the male morphs were previously considered as separate species: *Troxochrus scabriculus* (Westring 1851) and *Troxochrus scabriculus f. cirrifrons* (O.P.-Cambridge 1871); *Diplocephalus connatus* (Bertkau 1889) and *Diplocephalus connatus f. jacksoni* (O.P.-



Figures 1–3.—Carapace of 1. gibbosus morph male, 2. tuberosus morph male and 3. female of *Oedothorax gibbosus*.

Cambridge 1903); *Dicymbium nigrum* (Blackwall 1834) and *Dicymbium nigrum f. brevisetosum* (Locket 1962). The jumping spider *Maevia inclemens* (Walckenaer 1837) is also characterized by two male morphs; the morphology and courtship of these male morphs are so different that one would think that they belong to two different spider species (Clark & Uetz 1992,1993).

The elaborate structures present on the head of gibbosus males also occur in the males of many erigonine and other spider species. They have been analyzed morphologically for several species (Blest & Taylor 1977; Heinemann & Uhl 2000; Hormiga 2000; Huber 1997; Lopez 1976, 1987; Lopez & Emerit 1981; Meijer 1976; Schaible et al. 1986; Schaible & Gack 1987; Schlegelmilch 1974; Vollrath 1977). Schaible et al. (1986) suggests that the primary function of the male head structures in these erigonine spiders is to fix the position of the female during copulation. Their associated exocrine glands produce secretions, which females ingest during courtship and/or copulation. Schaible et al. (1986) were the first to suggest that the hairy groove in the gibbosus morph probably secretes a fluid that is important for the so-called gustatorial courtship, with the probable uptake of secretions by the female during courtship.

In order to observe and describe the normal courtship between a gibbosus male and *O. gibbosus* female as well as a tuberosus male and *O. gibbosus* female, we introduced a male spider into a vial (size: 5 cm diameter and 2,5 cm height) with a thin bottom of plaster containing the *O. gibbosus* female. The females had lived in these vials since they were first juveniles and had built a small web when a male of either morph was introduced. After the introduction of the male we observed the interactions for next 2 hours. We have observed over 100 courtships.

Typically, when a tuberosus male was placed in a vial with a female, the male moved his abdomen up and down, and approached the female. Sometimes the male cleaned his palps or moved in circles or in figure eight forms while moving his abdomen up and down. Sometimes these circles were around the female, but this was mostly not the case.

When a gibbosus male was placed with a female, he performed the same courtship behavior as described above, but gibbosus also exhibited the so-called gustatorial courtship. The gibbosus male approached the female or visa versa and allowed the female to insert her chelicerae into the hairy groove. Of the two morphs of *O. gibbosus* only the gibbosus male performed such gustatorial courtship; during this courtship the female exhibited movement of the chelicerae that appeared to be feeding behavior. Heinemann (1998) also studied this courtship behavior in this species.

Following courtship in both morphs, from a face-to-face position, the male shifted his cephalothorax underneath that of the female. In that way the two palps could easily reach the epigynum and the male inserted one or both palps successively. In the case of the gibbosus male, the transition of gustatorial courtship to copulation happened smoothly or with a break between courtship and copulation. During copulation most females removed their chelicerae from the hairy groove of gibbosus male. Fixation of the position for copulation as suggested by Schaible et al. (1986) is thus not the most important function of the male head structures of the *gibbosus* morph male. This is in contrast with other dwarf

Table 1.—First experiment in which an *Oedothorax fuscus* male or female was added to a pair consisting of an *O. gibbosus* female and a tuberosus male held in a small arena. The individuals between which courtship and copulation occurred and the duration of the copulation are given in the third and fourth column. The duration of the courtship is not given because this courtship was often interrupted. There were no interactions between the *O. fuscus* spider and the tuberosus male.

		Added	Courtship and copulation between	Duration copulation
1	*O. gibbosus* female & tuberosus male	1 *O. fuscus* male	tuberosus male & *O. gibbosus* female	67 min
			tuberosus male & *O. gibbosus* female	64 min
2	*O. gibbosus* female & tuberosus male	1 *O. fuscus* male	tuberosus male & *O. gibbosus* female	67 min
3	*O. gibbosus* female & tuberosus male	1 *O. fuscus* male	tuberosus male & *O. gibbosus* female	66 min
4	*O. gibbosus* female & tuberosus male	1 *O. fuscus* male	tuberosus male & *O. gibbosus* female	68 min
5	*O. gibbosus* female & tuberosus male	1 *O. fuscus* female	tuberosus male & *O. gibbosus* female	70 min

spider species wherein there is still contact between the female chelicerae and the male cephalic structures during copulation: *Hypomma bituberculata* (Wider 1834) (Bristowe 1931), *Walckenaeria corniculans* (O. P.-Cambridge 1875) (Schlegelmilch 1974), *Diplocephalus latifrons* (O. P.-Cambridge 1863) (Schlegelmilch 1974) and *Baryphyma pratense* (Blackwall 1861) (Blest & Taylor 1977). In *Walckenaeria cuspidate* Blackwall 1833 and *Gonatium rubellum* (Blackwall 1841) such contact only appears in the courtship (Schlegelmilch 1974).

For both male morphs, a successful copulation took more than an hour (Heinemann 1998; Vanacker unpub. data), during which first the contents of one palp is pumped into the epigynum followed by the contents of the second palp. Sometimes an incomplete copulation happened and a female received sperm from only one of the palps. There was no behavioral difference between a copulation of the two male morphs. The normal copulation position of the spiders was both spiders upside down under the web, the male above the female and the pattern of successively inserting the palps was similar for both morphs (Vanacker unpub. data). Because of the relative size of the hunch and because of the preponderance of gland cells in the hunch (unpubl. data) the production of the hunch and the hairy groove is evidently a high energy-investment for the gibbosus male. We expect that the gibbosus is probably the more sexually attractive male, but additional studies are necessary to confirm this.

The two male morphs always occur together in a population, but there is a variation in the male morph ratio between populations (Maelfait et al. 1990). It has been shown that the two morphs are determined by one gene with two alleles only expressed in the male sex (Maelfait et al.1990; Vanacker et al. 2001). The observation that the two male morphs coexist suggests that their fitness must be comparable. That the two male morphs occur together in many populations implies there may be a mixed evolutionary stable strategy, a mESS (Gadgil 1972; Maynard Smith 1982; Gross 1985; Shuster & Wade 1991; Eberhard & Guterriez 1991; van Rhijn 1991; Gross 1996; Tomkins & Simmons 1996; Schlinger et al. 1999; Simmons et al. 1999). As part of a larger study comparing the two morphs and examining several fitness characteristics we compared the response of females to each morph in the presence of a congener. Because the gibbosus male is apparently making a large morphological investment in reproduction, we expected that copulation with the gibbosus male would happen more quickly than with the tuberosus male and we expected there would be no interaction with the closely related species.

To test the response of females to each morph in the presence of another species, we set up the following experiment. An *O. gibbosus* female was put in a small transparent plastic vial (height: 2 cm, diameter: 5 cm) with a wetted thin layer of plaster of Paris and allowed to build a small web. To this individual, we added either a tuberosus or gibbosus male and one additional individual of another species (*O. fuscus* male or one *O. fuscus* female) (Table 1).

When we added to a tuberosus male and an *O. fuscus* male or female to an *O. gibbosus* female, courtship and mating happened only between the *O. gibbosus* female and the tuberosus male (Table 1). This courtship and mating behavior was not dis-

Table 2.—Second experiment in which different individuals were added (as indicated in the second column) to a pair of *Oedothorax gibbosus* female and a gibbosus male held in a small arena. The individuals between which a gustatorial courtship position occurred and the duration of that interaction are given in the third and fourth column.

		Added	Gustatorial courtship posture between	Duration
1	*O. gibbosus* female & gibbosus male	1 *O. fuscus* male	gibbosus male & *O. gibbosus* female	10 min
			gibbosus male & *O. fuscus* male	2 min
			gibbosus male & *O. fuscus* male	3 sec
			gibbosus male & *O. fuscus* male	2 sec
2	*O. gibbosus* female & gibbosus male	1 *O. fuscus* male	gibbosus male & *O. fuscus* male	5 min
			gibbosus male & *O. fuscus* male	2 min
			gibbosus male & *O. fuscus* male	6 sec
3	*O. gibbosus* female & gibbosus male	1 *O. fuscus* male	gibbosus male & *O. fuscus* male	6 min
			gibbosus male & *O. fuscus* male	4 min
4	*O. gibbosus* female & gibbosus male	1 *O. fuscus* female	gibbosus male & *O. fuscus* female	7 min
5	*O. gibbosus* female & gibbosus male	1 *gibbosus* male	gibbosus male & *gibbosus* male	12 min
6	*O. gibbosus* female & gibbosus male	7 *O. fuscus* males	gibbosus male & *O. fuscus* male	5 min
			gibbosus male & *O. fuscus* male	1 min
			gibbosus male & *O. fuscus* male	5 sec
			gibbosus male & *O. fuscus* male	30 sec
			gibbosus male & *O. fuscus* male	5 min
			gibbosus male & *O. fuscus* male	1 min
			gibbosus male & *O. fuscus* male	6 min
			gibbosus male & *O. fuscus* male	1 min

turbed by interactions of the male or female of *O. fuscus*.

However, the observations with the *O. gibbosus* female and the gibbosus male were completely different (Table 2). In this case, the intraspecific courtship behavior was disturbed by interspecific gustatorial behavior and copulation could not occur. In almost all of the interactions (Table 2), gustatorial courtship postures were between the gibbosus male and the *O. fuscus* male or female. In this experiment there was only one gustatorial courtship between an *O. gibbosus* female and a *gibbosus* male morph; in this case there did not follow a copulation. Curiously, apart from one normal pairing (top of table) all courtship postures were interspecific and/or intrasexual.

Finally, in the last experiment with the gibbosus morph, seven males of *O. fuscus* were introduced to make it even more difficult for *O. gibbosus* female to choose. In this experiment we expected an increase of interspecific courtships by several *O. fuscus* males; this was also the case and the gib-

bosus male could perform neither an intraspecific courtship nor copulation.

According to the lock and key hypothesis, the function of morphological differences in closely related species is the avoidance of time- and energy-expensive copulations between the species (Arnqvist 1998). A female could recognize a gibbosus morph male because of the nuptial gift in the hairy groove and can so distinguish them from males of other related dwarf spider, such as *O. fuscus*. A tuberosus morph would not need such courtship because it does not have typical cephalic structures like other related dwarf spiders and thus is already distinct from closely related species. The sexual selection hypothesis, in contrast, proposes that divergent evolution is the result of sexual selection, brought about by variation in paternity success among males. The differences in primary and secondary sexual traits between closely related species are than a consequence of this separated evolution in these reproductively separated species (Arnqvist 1998).

According to the lock and key hypothesis, the carapace structure of the gibbosus male would function to avoid meaningless sexual interactions in terms of fitness. Because of the observed interactions between gibbosus males and spiders of *O. fuscus*, this carapace structure of the gibbosus male apparently does not serve this function. This makes an alternative explanation for the evolutionary origin of these secondary sexual characters much more probable. Instead of resulting from selection due to interspecific interactions this alternative explanation tries to understand the origin of these differences in secondary sexual characters as being caused by an arms race between different genotypes of males for mating and fertilizations, thus due to a selection resulting from intraspecific interactions: sexual selection.

In the arena of sexual interaction (Alcock 1998), features can evolve by sexual selection that affect the female's (1) choice of a copulatory partner, (2) selection of sperm to fertilize her eggs and (3) production of offspring. These male traits can be of very different nature: visual, acoustic, tactile, olfactorial or gustatorial and are believed to offer cues to the female on which her mate choice can be based. The males accepted for copulation or the sperm that will be selected after copulation can be expected to produce the highest number or quality of offspring. Selection should favor female recognition of cues correlated with: (1) male health, (2) the genetic quality (good genes hypothesis), (3) sexual attractiveness of the male (Fisher's runaway selection hypothesis) and (4) material benefits (e.g., help in parental care, quality territories and nutrient transfer during copulation).

Transfer of food items or essential nutrients like salt and water during or directly after courtship and copulation in insects is called nuptial feeding (Alcock 1998). Hypotheses put forward for the current function of nuptial feeding in insects include prevention of cannibalism by females, attraction of females, copulation enticement, positioning of the female for coupling, prolongation of ejaculate transfer to counter the effects of sperm competition or paternal investment in offspring (Vahed 1998). Nuptial feeding for example happens in *Bittacus apicalis* (Mecoptera) (Thornhill 1976; Austad & Thornhill 1991) and the cockroach *Blattella germaianica* (Nojima et al. 1999). A spectacular example of nuptial feeding in spiders is the male of the red back spider that after penetration of the epigynum seemingly offers itself as a prey item by putting its abdomen very close to the chelicerae of the female who sometimes feeds on her (Forster 1992; Andrade 1996). Also relatively well studied is the offering of a prey item wrapped in silk by the male during courtship in *Pisaura mirabilis* (Clerck 1757), Pisauridae (Lang 1996; Nitzsche 1999; Stalhandske 2001). The cephalic structures occurring in many male erigonine spiders have not yet been studied in behavioral ecological and evolutionary context (e.g. not mentioned in Drengsgaard & Toft 1999 or Stalhandske 2001). The above-mentioned experiments suggest they should.

The hunch of gibbosus is completely filled with gland cells with different secretions (Vanacker, unpub. data), which strengthens the possibility that these gland cells secrete more than pheromones. Similar gland cells are found in other dwarf spider species like *Diplocephalus picinus* (Blackwall 1841) (Schaible et al.1986). Our above-cited experiments strongly suggest that these glands produce a secretion in the cephalic groove, which is attractive not only to conspecific females, but also to conspecific males and to males and females of a closely related species. However, combinations of gibbosus morph males with females and males of other erigonine genera (*Erigone* (Audouin 1826), *Gonatium* (Menge 1868)) did not lead to gustatorial behavior (Vanacker, unpub. obs.). The chemical composition of the secretion(-s) produced remains to be determined.

Sexual selection is more and more regarded as having the potential to play a major role in speciation (Panhuis et al. 2001). According to Arnqvist (1998), genital evolution is more than twice as divergent in groups in which females mate several times than in groups in which females mate only once. In *Oedothorax gibbosus* multiple mating is also common (Vanacker unpub. obs.). Sexual selection on secondary reproductive characters as in *Oedothorax gibbosus* may have been of importance in the speciation process in the species-rich genera of Erigoninae, e.g. *Walckenaeria* (Blackwall 1833), *Oedothorax* (Bertkau 1883) and *Diplocephalus*

(Bertkau 1883). We will study this last genus in this context in the near future.

Knowing the composition of the secretion of gibbosus might help in better understanding the function of that gustatorial courtship behavior: female attraction or copulatory enticement, prolongation of copulation or transfer nutrients to the male's offspring (paternal investment). It seems clear that gibbosus offers to the female a kind of nuptial gift made available in the hairy groove. The intrasexual and interspecific gustatorial courtship postures may then be interpreted as robbings of the nuptial gift.

We are indebted to Léon Baert, Lut Van Nieuwenhuyse, Domir De Bakker, Viki Vandomme and Katrijn Deroose for helping us catch the dwarf spiders in the field. This research could be realized thanks to a PhD grant of the Foundation for Scientific Research–Flanders.

LITERATURE CITED

Alcock, J. 1998. Animal behavior, an evolutionary approach. Sinauer Associates Publishers, Sunderland, Massachusetts.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton.

Andrade, M.C.B. 1996. Sexual selection for male sacrifice in the Australian redback spider. Science 271:70–72.

Arnqvist, G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. Nature 393:784–786.

Austad, S.N. & R. Thornhill. 1991. This bugs for you. Natural History 12:44–49.

Blest, A.D. & H.H. Taylor. 1977. The clypeal glands of *Mynoglenes* and of some other Linyphiid spider. Journal of Zoology London 183: 473–493.

Bristowe, W.S. 1931. The mating habits of spiders, a second supplement. Proceedings of the Zoological Society of London 4:1931.

Clark, D.L. & G.W. Uetz. 1992. Morph-independent mate selection in a dimorphic jumping spiders: demonstration of movement bias in female choice using video-controlled courtship behaviour. Animal Behaviour 43:2474–254.

Clark, D.L. & G.W. Uetz. 1993. Signal efficacy and the evolution of male dimorphism in the jumping spider *Maevia inclemens*. Proceedings of the National Academy of Sciences of the United Stated of America 90:11954–11957.

De Keer, R. & J.-P. Maelfait. 1988. *Oedothorax gibbosus* (Blackwall) and *Oedothorax tuberosus* (Blackwall): one species. Newsletter of the British Arachnological Society 53:3.

De Keer, R. & J.-P. Maelfait. 1989. Ecological backgrounds for the distribution patterns of *Oedothorax fuscus* (Blackwall) and *Oedothorax gibbosus* (Blackwall) (Erigoninae, Aranneae). Proceedings of the Symposium "Invertebrates of Belgium":189–192.

Drengsgaard, I. L. & S. Toft. 1999. Sperm competition in a nuptial feeding spider, *Pisaura mirabilis*. Behaviour 136:877–897.

Eberhard, W.G. & E.E. Guterriez. 1991. Male dimorphism in beetles and earwigs and the question of developmental constraints. Evolution 45: 18–28.

Forster, L.M. 1992. The stereotyped behavior of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae), the Australian redback spider. Australian Journal of Zoology 40(1): 1–11

Gadgil, M. 1972. Male dimorphism as a consequence of sexual selection. American Naturalist 106:574–580

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313(3):47–48.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in ecology and evolution 11:92–98.

Heinemann, S. 1998. Männchendimorphismus bei *Oedothorax gibbosus* (Blackwall) (Araneae: Linyphiidae): Morphometrie und Verhaltensuntersuchungen. Diplomarbeit der Universität Bonn.

Heinemann, S. & G. Uhl. 2000. Male dimorphism in *Oedothorax gibbosus* (Araneae, Linyphiidae): a morphometric analysis. Journal of Arachnology 28:23–28.

Hormiga, G. 2000. Higher level phylogenetics of erigonine spiders (Aranea, Linyphiidae, Erignoninae). Smithsonian Contributions to Zoology 609, 22 pp.

Huber, B. A. 1997. Evidence for gustatorial courtship in a haplogyne spider (*Hedypsilus culicinus*: Pholcidae: Aranae). Netherlands Journal of Zoology 47(1):95–98.

Lang, A. 1996. Silk investment in gifts by males of the nuptial feeding spider *Pisaura mirabilis* (Araneae: Pisauridae). Behaviour 133:697–716.

Lopez, A. 1976. Présence de glandes tégumentaires prosomatiques chez les mâles Erigonidae (Araneae). Comptes rendus de l'acedémie des Sciences Paris 282(D):365–367.

Lopez, A. 1987. Glandular aspects of Sexual Biology. Pp. 121–132. *In*: Ecophysiology of Spiders, W. Nentwig (ed),Springer-Verlag, Berlin.

Lopez, A. & M. Emerit. 1981. Le dimorphisme sexual prosomatique de *Walckenaeria acuminata* Blackwall, 1833 (Araneae, Erigonidae). Bulletin de la Société zoologique de France 106:125–131.

Maelfait, J.-P., De Keer, R. & L. De Meester. 1990. Genetic background of the polymorphism of *Oedothorax gibbosus* (Blackwall) (Linyphiidae, Araneae). Revue Arachnologique 9(2):29–34.

Maelfait, J.-P., Baert. L, Janssen, M. & M. Alderweireldt. 1998. A Red list for the spiders of Flan-

ders. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 68:131–142.

Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Meijer, J. 1976. A glandular secretion in the ocular area of certain erigonine spiders (Araneae, Linyphiidae). Bulletin of the British Arachnology Society 3(9):251–252.

Nojima, S., Sakuma, M., Nishida, R. & Y. Kuwahara. 1999. A glandular gift in the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): the courtship feeding of a female on secretions from male tergit glands. Journal of Insect Behaviour 12(5):627–640.

Nitzsche, R. 1999. Das Brautgeschenk der Spinne: *Pisaura mirabilis*. Rainer Nitzsche Verlag, Kaiserslautern, 254 pp.

Panhuis, T. M., Butlin, R., Zuk, M. & T. Tregenza. 2001. Sexual selection and speciation. Trends in Ecology and Evolution 16(7):364–371.

Roberts, M.J. 1987. The spiders of Great Britain and Ireland, 2: Linyphiidae. Harley Books, Colchester.

Schaible, U, Gack, C. & H.F. Paulus. 1986. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen männlicher Zwergspinnen (Linyphiidae: Erigoninae). Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere (Jena) 113:389–408.

Schaible, U. & C. Gack. 1987. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen einiger Arten der Gattung *Diplocephalus* (Araneida, Linyphiidae, Erigoninae). Verhandlungen des naturwissenschaftlichen Vereins in Hamburg (NF) (Hamburg); 29:171–180.

Schlegelmilch, B. 1974. Zur biologischen Bedeutung der Kopffortsätze bei Zwergspinnenmännchen (Microphantidae). Diplomarbeit Universität. Freiburg: 98 pp.

Schlinger, B.A., Greco, C. & A.H. Bass. 1999. Aromatase activity in the hindbrain vocal control region of a teleost fish: divergence among males with alternative reproductive tactics. Proceedings of the Royal Society of London Series B- Biological Sciences 266:131–136.

Shuster, S.M. & M.J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. Nature 350:608–610.

Simmons, L.W., Tomkins, J.L. & J. Hunt. 1999. Sperm competition games played by dimorphic male beetles. Proceedings of the Royal Society of London Series B- Biological Sciences 266: 145–150.

Stalhandske, P. 2001. Nuptial gift in the spider *Pisaura mirabilis* maintained by sexual selection. Behavioral Ecology. 12:691–697.

Thornhill, R. 1976. Sexual selection and nuptial feeding-behavior in *Bittacus apicalis* (Insecta, Mecoptera). American Naturalist 110:529–548.

Tomkins, J.L. & L.W. Simmons. 1996. Dimorphisms and fluctuating asymmetry in the forceps of male earwigs. Journal of Evolutionary Biology 9:753–770.

Vahed, K. 1998. The function of nuptial feeding in insects: review of empirical studies. Biological Reviews of the Cambridge Philosophical Society 73(1):43–78.

Vanacker, D., Maelfait, J.-P. & L. Baert. 2001. The male dimorphism in the dwarf spider *Oedothorax gibbosus* (Blackwall, 1841) (Erigoninae, Linyphiidae, (Araneae): results of laboratory rearing experiments. Belgian Journal of Zoology 131(Supplement 2):49–54.

van Rhijn, J.G. 1991. The ruff, individuality in a gregarious wading bird. Academic Press, New York.

Vollrath, F. 1977. Zur Ökologie und Biologie von kleptoparasitischen *Argyrodes* elevatus un synöken *Argyrodes*-Arten (Araneae, Theridiidae). Dissertation Universität Freiburg.

Manuscript received 18 March 2002, revised 18 December 2002.

ERRATUM

In Brookhart & Cushing (2002, Journal of Arachnology 39:84–97), the type locality for the male holotype of *Eremobates gerbae* was erroneously stated as: Rincon Mountains, Cochise County, Arizona, collected August–8 October 1995. The Rincon Mountains are in Pima county not Cochise County and the holotype was collected 30 August 1994. The female allotype of *E. gerbae* was also collected in the Rincon Mountains in Pima County and was collected on 8 October 1995.

INSTRUCTIONS TO AUTHORS

(revised September 2001)

General: Manuscripts are accepted in English only. Authors whose primary language is not English may consult the editors for assistance in obtaining help with manuscript preparation. All manuscripts should be prepared in general accordance with the current edition of the *Council of Biological Editors Style Manual* unless instructed otherwise below. Authors are advised to consult a recent issue of the *Journal of Arachnology* for additional points of style. Manuscripts longer than three printed journal pages should be prepared as Feature Articles, shorter papers as Short Communications.

Submission: Send four identical copies of the typed material together with copies of illustrations to the Managing Editor of the *Journal of Arachnology*: **Paula E. Cushing, *Managing Editor;* Denver Museum of Nature and Science, Zoology Department, 2001 Colorado Blvd., Denver, CO 80205-5798 USA** [*Telephone:* (303) 370-6442; *FAX:* (303) 331-6492; *E-mail:* PCushing@dmns.org]

The Managing Editor will forward your manuscript to one of the Subject Editors for the review process. You will receive correspondence acknowledging the receipt of your manuscript from the responsible Subject Editor or the Managing Editor, with the manuscript number of your manuscript. Please use this number in all correspondence regarding your manuscript. Correspondence relating to manuscripts should be directed to the Managing Editor or the appropriate Subject Editor. After the manuscript has been accepted, the author will be asked to submit the manuscript on a PC computer disc in a widely-used word processing program. The file also should be saved as a text file. Indicate clearly on the computer disc the word processing program used.

Voucher Specimens: Voucher specimens of species used in scientific research should be deposited in a recognized scientific institution. All type material must be deposited in a recognized collection/institution.

FEATURE ARTICLES

Title page. —The title page will include the complete name, address, and telephone number of the author with whom proofs and correspondence should be exchanged, a FAX number and electronic mail address if available, the title in capital letters, and each author's name and address, and the running head (see below).

Abstract. —The heading in bold and capital letters should be placed at the the beginning of the first paragraph set off by a period. A second abstract, in a language pertinent to the nationality of the author(s) or geographic region(s) emphasized, may be included.

Keywords. — Give 3-5 appropriate keywords following the abstract.

Text. —Double-space text, tables, legends, etc. throughout. Three levels of heads are used.

- The first level (METHODS, RESULTS, etc.) is typed in capitals and on a separate line.
- The second level is **bold,** begins a paragraph with an indent and is separated from the text by a period and a dash.
- The third level may or may not begin a paragraph but is italicized and separated from the text by a colon.

Use only the metric system unless quoting text or referencing collection data. All decimal fractions are indicated by the period (e.g., -0.123).

Citation of references in the text: Cite only papers already published or in press. Include within parentheses the surname of the author followed by the date of publication. A comma separates multiple citations by the same author(s) and a semicolon separates citations by different authors, e.g., (Smith 1970), (Jones 1988; Smith 1993), (Smith 1986, 1987; Smith & Jones 1989; Jones et al. 1990). Include a letter of permission from any person who is cited as providing unpublished data in the form of a personal communication. Citation of taxa in text: Please include the complete taxonomic citation for each arachnid taxon when it appears first in the paper. For Araneae, this taxonomic information can be found on-line at http://research.amnh.org/entomology/spiders/catalog81-87/INTRO2.html. For example, *Araneus diadematus* Clerck 1757.

Literature cited section. —Use the following style and include the full unabbreviated journal title.

Lombardi, S.J. & D.L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (dragline) of *Nephila clavipes* (Araneae, Tetragnathidae). Journal of Arachnology 18:297-306.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15-66, *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Footnotes.—Footnotes are permitted only on the first printed page to indicate current address or other information concerning the author. All footnotes are placed together on a separate manuscript page. Tables and figures may not have footnotes.

Running head.—The author's surname(s) and an abbreviated title should be typed all in capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style or contact the Subject Editor for Systematics. Papers containing the original taxonomic description of the focal arachnid taxon should be given in the Literature Cited section.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (usually three) should be included. Tables may not have footnotes; instead, include all information in the legend. Make notations in the text margins to indicate the preferred location of tables in the printed text.

Illustrations.—Original illustrations should not be sent until the article is accepted for publication. Address all questions concerning illustrations to the Editor of the *Journal of Arachnology*: **Dan Mott, *Editor-In-Chief*; Texas A&M International University, 5201 University Blvd., Laredo, TX 78041-1900 USA**; *E-mail:* dan.mott@tamiu.edu] All art work must be camera-ready – i.e., mounted and labeled – for reproduction. Figures should be arranged so that they fit (vertically and horizontally) the printed journal page, either one column or two columns, with a minimum of wasted space. When reductions are to be made by the printer, pay particular attention to width of lines and size of lettering in line drawings. Multiple photos assembled on a single plate should be mounted with only a minimum of space separating them. In the case of multiple illustrations mounted together, each illustration must be numbered sequentially rather than given an alphabetic sequence. Written on the back should be the name(s) of author(s) and an indication of top edge. Indicate whether the illustration should be one column or two columns in width. The overall dimensions should be no more than 11 inches (28 cm) x 14 inches (36 cm). Larger drawings present greater difficulty in shipping and greater risks of damage for which the *Journal of Arachnology* assumes no responsibility. In manuscripts for review, photocopies should be included, and should be reduced to the exact measurements that the author wants to appear in the final publication. Make notations in the text margins to indicate the preferred position of illustrations in the printed text. Color plates can be printed, but the author must assume the full cost, currently about $600 per color plate.

Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1-4.— *A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

Assemble manuscript for mailing.—Assemble the separate sections or pages in the following sequence; title page, abstract, text, footnotes, tables with legends, figure legends, figures.

Page charges, proofs and reprints.—There are no page charges, but the author will be charged for changes made in the proof pages. Reprints are available only from the Allen Press and should be ordered when the author receives the proof pages. Allen Press will not accept reprint orders after the paper is published. The *Journal of Arachnology* also is published by BioOne. Therefore, if your institution is a member of BioOne, copies of each article can be downloaded as PDF files.

SHORT COMMUNICATIONS

Short Communications are usually limited in length to three journal pages, including tables and figures. They will be printed in a smaller (10 point) typeface. The format for these is less constrained than for feature articles: the text must still have a logical flow, but formal headings are omitted and other deviations from standard article format can be permitted when warranted by the material being covered.

CONTENTS

The Journal of Arachnology

Volume 31 Featured Articles Number 2

Spiders of the genus *Tetragnatha* (Araneae, Tetragnathidae) in the Society Islands **by R.G. Gillespie** 157

Phylogenetic analysis of *Santinezia* with description of five new species (Opiliones, Laniatores, Cranaidae) **by Ricardo Pinto-da-Rocha & Adriano B. Kury** 173

On the use of ampullate gland silks by wolf spiders (Araneae, Lycosidae) for attaching the egg sac to the spinnerets and a proposal for defining nubbins and tartipores **by Mark A. Townley & Edward K. Tillinghast** 209

When to quit? Estimating spider species richness in a northern European deciduous forest **by Nikolaj Scharff, Jonathan A. Coddington, Charles E. Griswold, Gustavo Hormiga & Per de Place Bjørn** 246

Observations of *Theotima minutissmus* (Araneae, Ochyroceratidae), a parthenogenetic spider **by Robert L. Edwards, Eric H. Edwards & Annabel D. Edwards** 274

The effects of size, sex and reproductive condition on thermal and dessication stress in a riparian spider (*Pirata sedentarius*, Araneae, Lycosidae) **by Jill DeVito & Daniel R. Formanowicz, Jr.** 278

Clutch size and offspring size in the wolf spider *Pirata sedentarius* (Araneae, Lycosidae) **by Christopher A. Brown, Bridget M. Sanford & Rebekah R. Swerdon** 285

Natural history of *Misumenops argenteus* (Thomisidae): Seasonality and diet on *Trichogoniopsis adenantha* (Asteraceae) **by Gustavo Quevedo Romero & João Vasconcellos-Neto** 297

Short Communications

Effects of maternal body size on clutch size and egg weight in a pholcid spider (*Holocnemus pluchei*) **by Christa D. Skow & Elizabeth M. Jakob** 305

Is the hairy groove in the gibbosus male morph of *Oedothorax gibbosus* (Blackwall 1841) a nuptial feeding device? **by Danny Vanacker, Liesbeth Maes, Sylvia Pardo, Frederik Hendrickx & Jean-Pierre Maelfait** 309

Erratum

New species of Eremobatidae (Arachnida, Solifugae) from North America **by J.O. Brookhart & P.E. Cushing** 316

USERNAME: denver03 PASSWORD: spider03